CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS

REPORTS

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CONTENTS

Part I

REPORT, REVIEWS, AND PUBLICATIONS

REPORT OF THE CALCOFI COMMITTEE-1979

As of 1 January 1979, the legislative charter of the Marine Research Committee of the State of California expired. However, the principal working groups (the Southwest Fisheries Center of the National Oceanic and Atmospheric Administration, the California Department of Fish and Game, and the Marine Life Research Group at the Scripps Institution of Oceanography), through the CalCOFI Committee, will continue to collaborate and provide a medium for presenting research results. The CalCOFI Reports, Data Reports, and Atlases will continue to be available to the world scientific community.

Since our last Report in 1977, CalCOFI has produced Atlas Number 25, "Contoured Depth-Time Charts (0 to 200 m, 1950 to 1966) of Temperature, Salinity, Oxygen and Sigma-T at 23 CalCOFI Stations in the California Current," by L. E. Eber and Atlas Number 26, "Distributional Atlas of Fish Larvae in the California Current Region: Rockfishes, Sebastes spp.," by E.H. Ahlstrom, H. G. Moser, and E. M. Sandknop, as well as a number of Data Reports for the California Current.

CalCOFI is pleased to provide a forum in which researchers on various aspects of a common problem may be brought together. The symposium on the market squid, Loligo opalescens, reported in this volume, gives us new and valuable insights into the biology of reproduction, feeding, aging, and behavior of this important commercial species. New information on relationships between oceanographic conditions and larval survival may permit the prediction of catch potential and provide for better management of the stock. New information on squid school detection may aid fishermen to fish this species more effectively.

The excellent scientific and collegial relationships previously established with the Instituto Nacional de Pesca in Mexico have been enhanced by new programs of cooperative education and data sharing. The December 1977-August 1978 data collection cruises were performed by both Mexican and U.S. research vessels and scientists. This level of binational cooperation can provide the scientific foundation for good management of transboundary fisheries and certainly makes more economical use of ships and manpower in both nations.

Finally, the committee wishes to express its deep appreciation to Herbert Frey, of the California Department of Fish and Game, who has served as interim coordinator for some years. He is succeeded by George Hemingway of the Scripps Institution of Oceanography.

Isadore Barrett, John Radovich, Joseph Reid, George Hemingway.

REVIEW OF THE PELAGIC WET FISHERIES FOR 1976
WITH NOTES ON THE HISTORY OF THESE FISHERIES

Commercial wet-fish landings of pelagic species dipped from the 25-year high of 190,075 short tons in 1975 to 159,497 short tons during 1976 (Table 1). The lower anchovy catch was almost wholly responsible for the decrease in landings. Landings for all other species except squid showed increases over 1975. Squid landings decreased for the second straight year.

Northern Anchovy

Before 1952, anchovy landings in California seldom exceeded a thousand tons. The collapse of the sardine fishery in 1952 resulted in an increase in anchovy landings that were canned for human consumption. The temporary resurgence of the sardine fishery in 1954 and then again in 1958 resulted in corresponding decreases in anchovy landings. Catches remained low until 1966, presumably due to poor market conditions created by low consumer demand for canned anchovies. In 1965 the anchovy reduction fishery began, and landings averaged 73,000 tons/year during the next decade. A record 158,000 tons were landed in 1958; however, landings decreased during 1976 to 124,591.

The 1976 landings of anchovies (Table 1) include a portion of the landings for both the 1975-76 and 1976-77 anchovy reduction seasons (Table 2). Although the 1975-76 seasonal landings of 140,906 tons set a record, the large majority of this tonnage was landed before January 1976. From January 1 to the close of the season, May 15, 52,700 tons were landed, but in only 2 of the 13 weeks of fishing after January were cannery orders met.

In the northern permit area, final landings for the 1975-76 season totaled 5,295 tons. In the southern permit area, landings approached the initial quota of 100,000 tons in January, and the California Fish and Game Commission

granted an additional 50,000 tons. Final landings in the south were a record 135,615 tons. The anchovy price to the fishermen remained fairly stable at $28/ton in the north and $30/ton in the south during the winter and spring of 1976.

Sampling for age composition during the winter and spring of 1976 indicated that the anchovy biomass may have declined dramatically in recent years as a result of poor spawns during 1975 and 1974. The 1975 and 1974 year classes made up 4.8 and 9.0% of fish sampled between January 1976 and the end of the season. The 6-year average (1970-1975) of 1- and 2-year-old anchovies sampled during the same time of year is 19.1 and 32.3%.

The 1976-77 anchovy season opened on August 1 in the north and on September 15 in the south. Both fisheries began slowly.

In the northern permit area, anchovies were scarce in fishable concentrations during the first three months of the season, and fishing was seldom good after that period. By December 31 only 3,616 tons had been landed, and only four purse seiners and one lampara boat had made cannery deliveries. Price to the fishermen fluctuated between $40 and $42/ton during this period.

In the southern permit area, the season opened amidst a fisherman-aerial spotter dispute over shares and a fisherman-cannery price dispute. Most San Pedro reduction boats spent the last two weeks of September fishing bluefin tuna. Although canneries began receiving anchovies at both Terminal Island and Port Hueneme as early as September 16, fishermen were fishing on an "open ticket" while negotiating a price with canners. San Pedro fishermen closed fishing operations on October 6 while price negotiations continued. Fishing resumed on October 19 when San Pedro boat owners, fishermen, and Terminal Island canners reached agreement on a price of $39.75/

TABLE 1
Landings of Pelagic Wet Fishes in California in Short Tons 1964-76

Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
1964....	6,569	2,488	13,414	44,846	175	8,217	75,709
1965....	962	2,866	3,525	33,333	258	9,310	50,254
1966....	439	31,140	2,315	20,431	121	9,512	63,958
1967....	74	34,805	583	19,090	136	9,801	64,489
1968....	62	15,538	1,567	27,834	179	12,466	57,646
1969....	53	67,639	1,179	25,961	85	10,390	105,307
1970....	221	96,243	311	23,873	158	12,295	133,101
1971....	149	44,853	78	29,941	120	15,756	90,947
1972....	186	69,101	54	25,559	63	10,030	104,993
1973....	76	132,636	28	10,308	1,410	6,031	150,489
1974....	7	82,691	67	12,729	2,630	14,452	112,576
1975....	3	158,510	144	18,390	1,217	11,811	190,075
1976....	27	124,919	317	21,693	2,410	10,131	159,497

TABLE 2
Anchovy Landings for Reduction in the Southern and
Northern Permit Areas for 1966-67 through 1976-77 in Short Tons

Season	Southern permit area	Northern permit area	Total
1966-67	29,589	8,021	37,610
1967-68	852	5,651	6,503
1968-69	25,314	2,736	28,050
1969-70	81,453	2,020	83,473
1970-71	80,095	657	80,752
1971-72	52,052	1,374	53,426
1972-73	73,167	2,352	75,519
1973-74	109,207	11,380	120,587
1974-75	109,918	6,669	116,587
1975-76	135,615	5,291	140,906
1976-77*.......	101,434	5,007	106,441

*preliminary

ton. By October 31 only 17,300 tons had been landed compared with 40,000 tons during the same period of the previous season; however, fishing conditions were excellent during November and December, and by December 31 almost 70,000 tons had been landed. The price to the fishermen rose from $39.75 to $44.50/ton during this period.

Forty purse seines and five lampara boats applied for reduction permits in the south for 1976-77 season. By December 31, only two lampara boats and 35 purse seines had made cannery deliveries. Three of these purse seines were operating out of Port Hueneme.

Age composition data collected during the period September through November 1976 support the tenet of spawning failures during 1974 and 1975. One- and two-year-old fish (more accurately—1½- and 2½-year-old) traditionally have accounted for close to 70% of fish sampled during the fall of the year. In the fall of 1976, these age classes accounted for only 31% of the fish sampled.

Pacific Sardine

Fishing for sardines on the Pacific coast of North America began in 1889. The earliest records of landings in California are for the 1916-17 season, when less than 30,000 tons were landed. The next year a small fishery was initiated in British Columbia, and total sardine landings increased slowly until 1923-24, when about 85,000 tons were landed on the Pacific coast. The tonnage doubled in the 1924-25 season, and in subsequent years the fishery continued to grow, with development of the British Columbia fishery and the rapid expansion of California fisheries. In 1935, sardine fishing began in Washington and Oregon, and in the 1936-37 season approximately 791,000 tons were landed. The fishery remained productive over the next eight years, with landings fluctuating between 500,000 and 680,000 tons. During this period, however, the catch per unit of effort was declining, and the period 1944 to 1947 was accompanied by a sharp drop in landings. During the subsequent three years, the fisheries in British Columbia, Washington, and Oregon were discontinued, although California had increased its landings slightly. Disaster struck the sardine industry in 1952 and 1953, when less than 25,000 tons were landed in California during the 2-year period. By this time, a small Mexican fishery was in operation out of Ensenada, Baja California.

In retrospect, the disaster of the early 1950's marked the end of an era in the history of California fishing. Sardine landings have never again reached the levels of the 1940's, although slight revivals occurred in 1954 and 1958. The fishery continued to decline after the 1958-59 season, and following 1965 the reported catch has never exceeded 500 tons/year in California (Table 1).

By the early 1960's, the sardine was no longer abundant enough to be of much value to the canning and reduction industries. As fishermen and industry turned to substitute species, such as jack mackerel and northern anchovies, fishing pressure on sardines normally would have been expected to subside enough to allow the opportunity for a resurgence of the population. However, fishermen continued to take sardines when and where they could. Although their catches were seldom more than a few tons, the sardine was considered a prime bait fish by sportsmen, with dealers paying $400 to $500/ton for them. Thus, when fishermen were unable to catch large amounts of less valuable pelagic species, a few tons of sardines could "make a boat's day."

In 1967, California passed legislation that sought to diminish the fishing pressure on an already badly depleted resource. It provided that no sardines may be taken or possessed on any boat, except that loads or lots of fish may contain 15% or less by weight of sardines. In 1969, new legislation provided for a 250-ton annual quota in addition to the existing incidental catch restriction. In 1973, a sardine management bill was passed that provided for a sardine moratorium until the spawning population reaches 20,000 tons.

The sardine population has been in a depressed state now for close to three decades, and it has been 15 years since the last "sizeable" landings of 25,000 tons during the 1961-62 season. The value of these landings must have seemed paltry compared to the almost 800,000 tons landed during the 1936-37 season.

During 1976, an estimated 14 tons of sardines were caught and landed incidental to other fishing operations (Table 1).

Pacific Mackerel

For a span of five decades, during the 20th century, Pacific mackerel supported one of California's more important commercial fisheries. Briefly, the cannery fishery began in the mid-1920's. Landings increased rapidly and peaked in 1935, when 73,000 tons were processed. This was followed by a steady decline in the catch, which dipped to 3,750 tons in 1953. During the next 11 years, landings averaged 17,000 tons/year. After 1964 the fishery experienced a rapid decline until, for all practical purposes, it ceased to exist at the beginning of this decade (Table 1). At this time (1970) the California Legislature passed a bill establishing a moratorium on the commercial fishing of Pacific mackerel, limiting catches to only incidentally caught fish. In 1972 this legislation was renewed and included management provisions for the opening of the fishery when the spawning biomass reached 10,000 tons.

During 1976 an estimated 169 tons of Pacific mackerel were caught and landed incidentally to other fishing

operations. This is a minimum estimate and was calculated from observation of only a portion of the incidental landings of Pacific mackerel. The assumption that considerably more Pacific mackerel were landed during 1976 is not a poor one as the frequency of occurrence of these fish in jack mackerel landings was dramatically higher than in more recent years.

Age and length composition data collected during 1976 indicate that the increased catches were the result of a relatively successful spawning during 1974. Although these same data indicate the 1975 spawning season was a failure, they and other data suggest the 1976 spawning season was a dramatic success.

In August and September 1976, live-bait fishermen from Oxnard to San Diego were reporting the frequent occurrence of young-of-the-year Pacific mackerel in their catches. In the last 15 years, including 1974 (a relatively successful spawning season), the occurrence of these juveniles mixed incidentally with live-bait catches was considered a rare event. The widespread nature of these occurrences was enough to suggest that the 1976 spawning season was a success. By October the juvenile Pacific mackerel had moved offshore and disappeared from live-bait catches but began occurring frequently in anchovy reduction landings. This was considered as another good sign, as Pacific mackerel have been seen only rarely in anchovy reduction landings. The first quantifiable evidence of a successful spawn was gathered on a California Department of Fish and Game (CDFG) research cruise during November, when juvenile Pacific mackerel were collected in 37% of the midwater trawls. This was the highest trawl success ratio for Pacific mackerel since the inception of CDFG midwater trawl surveys in 1962. By December the 1976 year class was being caught and landed incidentally with jack mackerel at Terminal Island canneries.

Because few Pacific mackerel are known to mature at the age of one year, a sizeable fishery is not expected until 1978.

Jack Mackerel

Historically, jack mackerel were of minor commercial importance before 1947. During that year a decrease in sardine catches resulted in a rapid expansion of the jack mackerel fishery.

Since its inception the jack mackerel fishery seems to have fluctuated more as a result of market conditions, cannery capacities, and availability of other species than as a result of variations in biomass levels. During the first eight years of the fishery, landings averaged 46,000 tons. Landings dropped off considerably in 1954 and 1958 due to the temporary resurgence of sardines in those years. With the subsequent decline of the sardine, landings increased and averaged 40,000 tons/year from 1960-65.

With the beginning of the anchovy reduction fishery in 1965, landings of jack mackerel decreased and averaged approximately 27,000 tons from 1966 to 1972 (Table 1). A sharp drop in landings was evidenced in 1973 and was mostly attributed to a good local bluefin tuna season and poor weather on offshore banks. In January 1974 the major cannery for jack mackerel was destroyed in a fire, and landings since then have remained relatively low.

During 1976 jack mackerel fishing was termed "excellent" by most fishermen. Although good weather conditions during most of the year played a part, fishermen indicated that it was the increased availability of jack mackerel in nearshore waters that made fishing so good. This year departed from the trend in more recent years which showed an increase in landings from the offshore areas of San Clemente Island and from Cortes and Tanner Banks. Even with reduced cannery capacities, the 1976 landings reached a 4-year high of 22,300 tons (Table 1). Jack mackerel price to the fishermen was stable during most of the year at $85/ton.

Pacific Herring

Pacific herring landings have shown three distinct peaks since records of the landings were first tabulated in 1916.

Due to the demand for food during World War I, landings averaged 2,800 tons from 1916 to 1919. In 1948 and from 1951 to 1953 landings averaged 3,800 tons. This peak in landings developed to fill the demand created by the scarcity of sardines off central California, and the majority of these fish were canned for human consumption. From 1973 to 1976, landings averaged 1,900 tons (Table 1). This fishery developed as the result of the demand for herring roe in Japan. In the years between these peaks, landings seldom reached more than a few hundred tons.

During 1976 herring were fished in Tomales Bay and San Francisco Bay under a permit system. The fisheries in both bays were regulated by season closures and quota levels for the different types of gear: purse seines, lampara nets, and gill nets. Limited entry was operative for both fisheries, with drawings held to determine permit holders. Although quotas were set at 3,050 tons for San Francisco Bay and 625 tons for Tomales Bay, the respective landings were only 1,654 tons and 144 tons. The primary reason quotas were not reached was because the major spawning runs were over before fishing began. Approximately 570 tons were landed outside these bays, bringing the total 1976 landings to 2,366 tons.

Sampling for length and sex composition during the 1976 season showed that gill nets caught larger fish and a higher proportion of females than did round haul nets.

Market Squid

Before 1943 squid landings in California were rarely more than a couple of thousand tons. In 1946, a record of 19,000 tons were landed as a result of an abnormally high demand by various federal and international aid programs. Since 1946, landings have fluctuated between 1,300 tons in 1960 to 16,000 tons in 1971. During the 1950's, landings north of Point Conception dominated the catch. From 1961 to 1972 landings north and south of Point Conception were approximately equal. The average yearly landings during this period were 5,000 tons in the north and 4,500 tons in the south. In 1973 landings dropped sharply due to low availability of squid in Monterey Bay. Landings increased to over 7,000 tons in the north during 1974, but fewer than 2,500 tons were landed in 1975 (Table 1). Catches in the south during these years, 1973 to 1975, varied less, fluctuating between 5,000 and 8,000 tons.

Monterey squid fishermen experienced another poor season during 1976, as landings reached only 2,511 tons. Landings decreased slightly south of Point Conception for the first time in four years, as approximately 7,620 tons were landed.

Richard A. Klingbeil

REVIEW OF THE PELAGIC WET FISHERIES 1977

Total commercial landings of pelagic wet fishes increased in 1977, even though the largest fishery, northern anchovy, experienced a decline. The resurgence of the Pacific mackerel resource resulted in a 13-year high in its landings. Increased effort and favorable market conditions were partly responsible for a 25-year high for jack mackerel landings and a record high for Pacific herring landings. Market squid landings increased substantially over 1976, when southern California fishermen experienced a record year.

Northern Anchovy

The 1977 landings of anchovies (Table 1) include a portion of the landings for both the 1976-77 and 1977-78 anchovy reduction seasons (Table 2).

As of January 1, 1977, Monterey fishermen had caught 3,791 tons of a 15,000-ton quota. In the southern permit area (south of Point Buchon), San Pedro and Port Hueneme seiners had landed 67,330 tons toward a 100,000-ton quota. The three boats fishing out of Port Hueneme accounted for approximately 22% of this tonnage.

Fishing began very slowly after inclement weather greeted the new year. Landings remained low in both areas, with southern area fishermen complaining of poor availability of fishable concentrations and Monterey fishermen diverting their efforts toward Pacific herring. Cannery orders at Terminal Island were not met until the second week of March, when a catch rate of approximately 1,200 tons/day was sustained for 19 days. After April 1, San Pedro fishermen were again unable to fill cannery orders. Port Hueneme fishermen were even less successful as they accounted for less than 5% of the tonnage landed between January 1 and May 15, season closure. Monterey fishermen were also unsuccessful in locating good concentrations of anchovies during the spring of 1977.

On March 31, the California Fish and Game Commission increased the southern area quota to 120,000 tons. Landings declined almost immediately, and the 1976-77 season closed May 15 with 101,434 tons and 5,007 tons being landed in the southern and northern permit areas, respectively.

A maximum of 33 and 4 boats participated in landings in the south and north, respectively, during the winter and spring of 1977. The price during this period fluctuated between $50-55/ton in the north and $48-57/ton in the south, with the highest prices being offered at the season's end.

Age composition of samples during the spring of 1977 supported previous conjecture that the 1974 and 1975 year classes were relatively weak. They represented less than 25% by number of all fish sampled compared with an average of well over 40% for 2- and 3-year-old fish during previous spring fisheries.

The 1977-78 season opened August 1 in the northern permit area (15,000-ton quota) and September 15 in the south (100,000-ton quota). Landings in both areas were substantial during most of the late summer and fall months.

Eleven Monterey boats (six seiners and five lampara vessels) participated in the best fall reduction fishery since 1973. Landings reached 7,136 tons by December 30, 1977, although effort was reduced somewhat by intermittent price disputes. The anchovy price at Monterey fluctuated between $35 and $41/ton during the fall, closing out the year at $40.25/ton.

In the southern permit area, the 1977-78 season opened amidst controversy. Although Port Hueneme boats (three purse seiners) began fishing immediately,

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Year	Pacific sardine	Northern anchovy	Pacific mackerel	Jack mackerel	Pacific herring	Market squid	Total
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1966....	439	31,140	2,315	20,431	121	9,512	63,958
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1969....	53	67,639	1,179	25,961	85	10,390	105,307
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1974....	7	82,691	67	12,729	2,630	14,452	112,576
1975....	3	158,510	144	18,390	1,217	11,811	190,075
1976....	27	124,919	317	21,693	2,410	10,131	159,497
1977*	4	111,476	5,930	49,453	5,826	14,121	186,810

*preliminary

TABLE 2

Anchovy Landings for Reduction in the Southern and Northern Permit Areas for 1966-67 through 1977-78 in Short Tons

Season	Southern permit area	Northern permit area	Total
1966-67	29,589	8,021	37,610
1967-68	852	5,651	6,503
1968-69	25,314	2,736	28,050
1969-70	81,453	2,020	83,473
1970-71	80,095	657	80,752
1971-72	52,052	1,314	53,426
1972-73	73,167	2,352	75,519
1973-74	109,207	11,380	120,587
1974-75	109,918	6,669	116,587
1975-76	135,615	5,291	140,906
1976-77	101,434	5,007	106,441
1977-78*	68,477	7,211	75,688

*preliminary

the majority of the San Pedro fleet remained idle, as only one cannery at Terminal Island had agreed to a price ($38/ton). By the end of September, all canneries were in operation and were paying $41.25/ton. The price fluctuated between $41 and $43/ton for most of the fall. Fishing success was good for both fleets during the fall months, although daily landings declined somewhat in December. A maximum of 37 purse seiners participated in landings at Terminal Island. The Port Hueneme seiners landed 19% of the 67,414 tons caught between September 15 and December 31, 1977.

The 1974 and 1975 year classes continued to be poorly represented in sampled landings. Samples were predominated by 1-year-olds (1976 year class), which accounted for approximately 38% of individuals sampled.

During 1977 an estimated 983 tons of anchovies were landed for nonreduction purposes, i.e. canning, frozen bait, fresh-fish markets. An additional 7,066 tons are estimated to have been used for live-bait purposes.

Pacific Sardine

The moratorium on taking Pacific sardines remained in effect with fewer than five tons being landed incidentally with mackerels. Sardines were rarely seen during 1977, occurring in fewer than 1% of mackerel cannery landings. Live-bait fishermen only rarely reported seeing any young-of-the-year, "firecrackers," as the central population continued to remain in a very depressed state.

Pacific Mackerel

Fishermen will long remember 1977 as the year of the return of the "blue mackerel." As a result of an extremely successful 1976 spawning season, a large 1976 year class became fully vulnerable to the purse seine fishery during 1977.

Pacific mackerel frequently school with jack mackerel, and during the first few months of the year the tonnage landed incidental to jack mackerel landings increased dramatically. During this period of time a moratorium continued to regulate the commercial catch of Pacific mackerel, and fishermen were only allowed to land loads that contained 18% or less by weight of "blues." However, during May the mixture of Pacific mackerel became of such a magnitude that fishermen indicated the "blues" were interfering with the jack mackerel fishery. Jack mackerel landings did decrease in May, and fishermen complained they frequently had to "dump" loads that had too high a proportion of Pacific mackerel.

On June 8, emergency legislation was passed permitting an increase in the incidental catch of Pacific mackerel to 40% by weight. This law also permitted pure loads to be landed if they did not exceed three tons and provided that only the pure loads and the tonnage landed that exceeded 18% by weight in mixed loads would be counted against

the quota to be established for the 1977-78 season beginning October 1.

During the remainder of the year, approximately 4,400 tons were landing bringing the 1977 annual landings to an estimated 5,930 tons. This total represents the highest annual landings since 1964 when 13,414 tons were landed.

In December 1977 the California Department of Fish and Game recommended a 5,000-ton quota be officially established for the 1977-78 season (October 1-September 30).

Jack Mackerel

Landings during 1977 reached a 25-year high of 49,453 tons. This is more than double the average annual landings between 1965 and 1976. The record landings occurred in 1952 when 73,261 tons were caught.

Several factors have influenced the increase in landings during 1977. During February the major cannery for jack mackerel, which had been destroyed by fire in 1974, began operation again, and another cannery began processing jack mackerel for the first time. Anchovy fishing from January to May and bluefin tuna fishing during the summer were below expectations, resulting in more effort being expended on jack mackerel. The southern California fishing industry was encouraged to take more jack mackerel because of the possible future allocation of tonnage to foreign fleets. Availability of jack mackerel on traditional fishing grounds remained high during most of the year, and the price, which began at $95/ton, rose to $100 early in the year and remained stable. Landings might have been considerably higher if market conditions had not been depressed in August through October, resulting in reduced cannery orders. The low tolerance for Pacific mackerel caught incidentally with jack mackerel may have also reduced landings in the spring.

Size and age composition data indicated that two year classes (1974 and 1976) contributed to the bulk of the tonnage landed. The 1975 year class was poorly represented, and it now appears that 1975 was a weak spawning year for both mackerels as well as for the northern anchovy.

Pacific Herring

During 1977 California's herring landings reached a record high of approximately 5,826 tons. The previous high of 4,748 tons was landed in 1952 and was the result of increased demand for alternative species, created by a scarcity of Pacific sardines.

The herring fishery continued to be regulated by seasonal quotas by area—San Francisco (4,015 tons), Tomales (825 tons), Bodega (250 tons), and Humboldt (50 tons) Bays. In addition, quotas were allocated by gear (round haul and gill net) in San Francisco and

11

Tomales Bays. In Bodega and Humboldt Bays only gill nets were allowed. The Tomales Bay fishery operated on a limited-entry basis, with a drawing for seventeen permits. A total of 230 and 24 permits were issued for San Francisco and Bodega Bays, respectively.

Market Squid

California's squid fishery is best summarized in terms of landings north and south of Point Conception. To the north the catches are landed primarily at Monterey, historically a summer fishery. In the south, historically a winter fishery, San Pedro is the major port of delivery, with substantial landings taking place at Port Hueneme.

Monterey fishermen had their fourth poor year out of the past five years and their third straight season when landings have fallen below 3,000 tons. Squid failed to show up on traditional fishing grounds during the early summer, and it was not until late summer and early fall that good catches were made by the lampara boat fishery. Annual landings are estimated at 2,234 tons.

Almost directly opposed to the trends in the north, landings in the south have increased in five out of the last six years, and during 1977 a record 11,887 tons were landed in spite of a relatively poor 1977 winter season, cut short by frequent storms. The record resulted primarily from unseasonably high landings during the summer and the early start of the 1977-78 winter season. More than 70% of the landings occurred in four months: January, August, November, and December.

Richard A. Klingbeil

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July 1, 1976 to June 30, 1978

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Part II

SYMPOSIUM OF THE CALCOFI CONFERENCE

INDIAN WELLS, CALIFORNIA
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THE MARKET SQUID, *LOLIGO OPALESCENS*

PELAGIC ASSEMBLAGES AS DETERMINED FROM PURSE SEINE AND LARGE MIDWATER TRAWL CATCHES IN MONTEREY BAY AND THEIR AFFINITIES WITH THE MARKET SQUID, *LOLIGO OPALESCENS*

GREGOR M. CAILLIET
Moss Landing Marine Laboratories
P.O. Box 223
Moss Landing, CA 95039

KONSTANTIN A. KARPOV
The Resources Agency
California Department of Fish and Game
California State Fisheries Laboratory
350 Golden Shore
Long Beach, CA 90802

DAVID A. AMBROSE
National Marine Fisheries Service
1140 North Harbor Drive
San Diego, CA 92101

ABSTRACT

The catches of large midwater trawls and commercial anchovy purse-seine hauls were analyzed for recurrent assemblages of pelagic organisms in Monterey Bay. In all, 71 samples, taken in the upper 50 fathoms using large (30-and 50-foot-mouth) midwater trawls aboard the R/V *Alaska* were examined. For the years 1968 to 1974, species composition data were obtained from California Department of Fish and Game records and the CalCOFI data report series. Original data were used in the 1975 and 1976 surveys. From similar depths and locations in 1975 and 1976, 29 commercial anchovy hauls were subsampled as they were being unloaded in Moss Landing Harbor. Due to the differences in sampling methods, data for individual taxa are presented only as presence or absence, relative abundance, and frequency of occurrence. Ranks of relative abundance for the dominant taxa are presented for both methods. In addition, catches were subjected to recurrent group analysis, and both methods showed similar assemblages despite the obvious differences in purpose of sampling and the type of gear employed. Catches taken over deeper water (more than 35 fathoms, or 64 m) were compared with those from shallower water, and the differences are discussed. In general, catches were dominated by *Loligo opalescens* and *Engraulis mordax*, but other frequently occurring organisms were *Sebastes* spp., *Merluccius productus,* scyphomedusae (*Pelagia* and *Chrysaora*), *Torpedo californica, Citharichthys sordidus, Porichthys notatus, Genyonemus lineatus, Peprilus simillimus,* and *Clupea harengus pallasii.*

INTRODUCTION

Although many studies have assessed various parameters of populations of commercially fished pelagic organisms such as anchovies, mackerels, and squid (Messersmith 1969, Mais 1974b), few have considered those organisms that commonly co-occur with these species. To adequately manage a commercially exploited species, it is important to consider the associated organisms comprising the biological component of its ecosystem, especially those involved in such important ecological interactions as predation and competition for food and space. It was this assumption, among others, that led Kato and

Hardwick (1975) to propose that "research is needed on economics, population dynamics, distribution and life history of *Loligo opalescens* in order to expand the fishery with due regard to optimum sustainable yield, economic ramifications and the ecosystem." It is our objective in this paper to present preliminary studies on the biological ecosystem of the market squid population in Monterey Bay.

Techniques such as midwater trawling and purse seining can be useful in exploratory fishing (Blackburn and Thorne 1974), in assessing distribution and abundance patterns, in assessment of recurrent pelagic assemblages, and in identifying potential competitors and predators (Day and Pearcy 1968; Fager and Longhurst 1968). An additional benefit from such sampling techniques would be the determination of the non-target species that are captured but not utilized by a fishery employing these types of gear. Also, Kato and Hardwick (1975) have suggested that commercially "alternate fishing methods—such as bottom and midwater trawling—may prove to be fruitful in some areas or seasons, particularly with the non-spawning squid."

Preliminary subsampling of northern anchovy commercial purse seine operations out of Moss Landing, California, showed that catches included numerous other species, including *Loligo opalescens.* We decided that an assessment of pelagic assemblages would be possible by subsampling these catches at the offloading dock. In addition, the California Department of Fish and Game (CDFG) Sea Survey Program has been using large midwater trawls since 1966 to estimate northern anchovy population abundance and distribution. The data from these samples are available and can be used in determining which organisms tend to associate with each other and with the market squid in the pelagic waters off central California. Recently, the same gear has been used on several successive summer CDFG cruises to evaluate the market squid resource and to obtain specimens for further natural history studies (Ally 1974, 1976; Ally and Mais 1975).

Thus, using subsamples from commercial anchovy purse seine catches and from larger midwater trawl samples from the CDFG Sea Survey, coupled with three successive CDFG summer squid cruises using the same

gear, we here attempt to characterize the pelagic nekton assemblages in Monterey Bay, especially with reference to their allegiance to the market squid, *Loligo opalescens*, in these samples.

MATERIALS AND METHODS

Commercial anchovy hauls from five different fishing boats were subsampled from September 1975 through March 1976. All sets were at night, using purse seines and lampara nets with mesh sizes ranging from ⅝-inch (16 mm) to ¾-inch (19 mm) square mesh and measuring from 165 feet (50.3 m) to 1,500 feet (454.5 m) in length. The methods of fishing followed those described in Messersmith (1969). Fishing intensity varied daily with the number of sets per night ranging from one to four and over the season sampled with four boats operating from September through November. Only one boat operated the remaining four months. Subsamples were taken as the boats were off-loading the total night's catch at either the Starkist or Santa Cruz Cannery docks in Moss Landing, California. The catches were brailed or sucked out of the boat's hold onto a conveyor belt heading toward the cannery for processing. As the catch was moving up the conveyor at a rate varying from ½ to 1 ton/minute, the organisms were visually inspected for alternate 5-ton intervals for the duration of the off-loading period. All organisms were identified to as low a taxon as possible and enumerated. Those species that were difficult to identify on sight were saved for later identification in the laboratory. In an attempt to quantify the visual inspection techniques, intermittent 5-gallon bucket samples (averaging 40 pounds of organisms) were taken at the end of the conveyor belt. The organisms contained in these samples were sorted, identified and enumerated, and conversion factors were calculated so that the numbers seen visually on the belt coincided with the numbers sampled in the buckets. Since it was necessary only to express abundances relatively (as percent by number and frequency of occurrence), estimates of density such as numbers per ton were not required and the sampling program as designed proved sufficient. In order to assess the effect of depth of the samples and their proximity to the Monterey Submarine Canyon, the sample depths were divided into those that were in waters deeper than 64 m (35 fathoms) and those shallower than 64 m.

Information on organisms captured by midwater trawl was gathered in two ways. First, on three cruises during the summers of 1974, 1975, and 1976 (Ally 1974, 1976; Ally and Mais 1975), samples were taken using a large midwater trawl with a mouth opening 11.6 to 13.7 m (38 to 45 feet) (Mais 1974b) aboard the CDFG R/V *Alaska*, following methods described by Ally and Mais (1975). Tow durations ranged between 5 and 15 minutes, with most being between 5 and 7 minutes. Depths trawled ranged from 44 to 166 m and all were taken at night,

usually between 2200 and 0300 hours. All organisms captured in these tows were sorted, identified to the lowest possible taxa, and enumerated. For those species that were not very abundant, all individuals were separated and counted. For the more numerous and usually smaller species, subsamples of the residue were taken, sorted, identified, and enumerated until the mean number per subsample agreed between one sample and the next and their standard deviations became minimal. These means were then raised by a factor to convert the sample numbers to total abundance in the tow, so that all species could then be ranked according to their proportionate number. Again, as with the anchovy haul subsamples, abundance was expressed as percent by number and frequency of occurrence, not as number per tow or minutes towed, due to the difficulty in obtaining the latter estimates.

The second source of midwater trawl information was the CDFG Sea Survey species composition and abundance data from midwater trawling surveys conducted from 1968 through 1975 and tabulated in the CalCOFI Data Reports (Mais 1971a-c, 1972, 1973, 1974a, 1975, 1976). Much of this information, especially for northern anchovy populations and acoustic monitoring, is summarized by Mais (1974b). However, as with the three summer cruises for squid, midwater trawl samples had been sorted to species and their relative abundances estimated. These data could then be retrieved from the CalCOFI Data Report for each year and location of interest. Data on all organisms captured in tows that were in the Monterey Bay vicinity (see Figure 3) were extracted and analyzed for species composition. The results were separated into summer tows that were either shallow (shallower than 64 m) or deep (deeper than 64 m) and winter tows, which were of mixed depths. To justify lumping data from both sources of midwater trawls, a species-by-species comparison between our data from both the three summer cruises and the particular CalCOFI Data Report for that year was made and indicated that the two were virtually identical. This enabled our trawl survey to cover a wide range of years, from 1958 through 1976.

The sufficiency of the number of samples was evaluated by plotting the cumulative number of species captured against the randomly-ordered number of subsamples both for anchovy hauls and midwater trawl hauls. These curves were visually inspected for the point at which more samples did not increase the cumulative number of species substantially. Since we were only interested in relative abundance and the presence or absence of a particular taxon, and since most taxa that were encountered toward the end of the cumulative curve were extremely rare, this method is sufficient to assess the minimum number of samples needed to evaluate species composition.

Abundances of the invididual taxa from all collection

methods were expressed as percent frequency of occurrence (that proportion of samples containing the taxon) and percent by number (the numerical proportion of all organisms captured that were of a specific taxon). For the tables showing abundance, only those species that were "common" (having a numerical importance of at least 0.01) were included. In the case of the commerical anchovy hauls, northern anchovy counts were excluded from the calculations so that the relative proportions of other species would be detectable. The species composition of samples from commercial anchovy hauls and midwater trawls was then described using the total number of common species captured and the percent dominance (the sum of the individual percentages by numbers squared [Odum 1971]). Species similarity was compared among depths and methods using the equation $S = \dfrac{2C}{A + B}$ where C is the number of species common to both samples and A and B are the number of species found in samples A and B, respectively (Odum 1971).

In addition, for each of the methods and depths studied, recurrent group analysis was performed after Fager (1957) and Fager and McGowan (1963). In this analysis, the index of affinity (I) was calculated between each pair of species over all samples using the formula

$$I = [J/(N_A N_B)^{1/2}] - \frac{1}{2}(N_B)^{1/2}$$

where N_A and N_B are the numbers of occurrences of species A and B, and J is the number of joint occurrences of both species, and where N_B is larger than N_A. Using a minimum value of 0.5, a matrix of significant I values is generated that enables a process to resolve major groups of organisms that commonly occurred with each other. Finally, in order to identify potential interspecific relations, the index of affinity of each of the dominant organisms with *Loligo opalescens* was calculated.

RESULTS

Species Composition: Anchovy Hauls

Subsamples from anchovy hauls were taken from 6 deep and 23 shallow locations, representing approximately 557 tons, during September through March 1975 (Figure 1, Table 1). The cumulative species curve leveled off at around eight hauls and remained level until 16 hauls, when four new species occurred (Figure 2). These four, *Pleuronichthys decurrens, Sardinops caerulea, Alopias vulpinus* and *Psettichthys melanostictus,* were not representative of the species commonly occurring in these hauls, since single individuals were captured only once. Therefore, it appears that approximately eight hauls were sufficient to adequately represent the species composition of pelagic organisms from anchovy hauls. The total number of taxa found in anchovy samples was 22 (Figure 2).
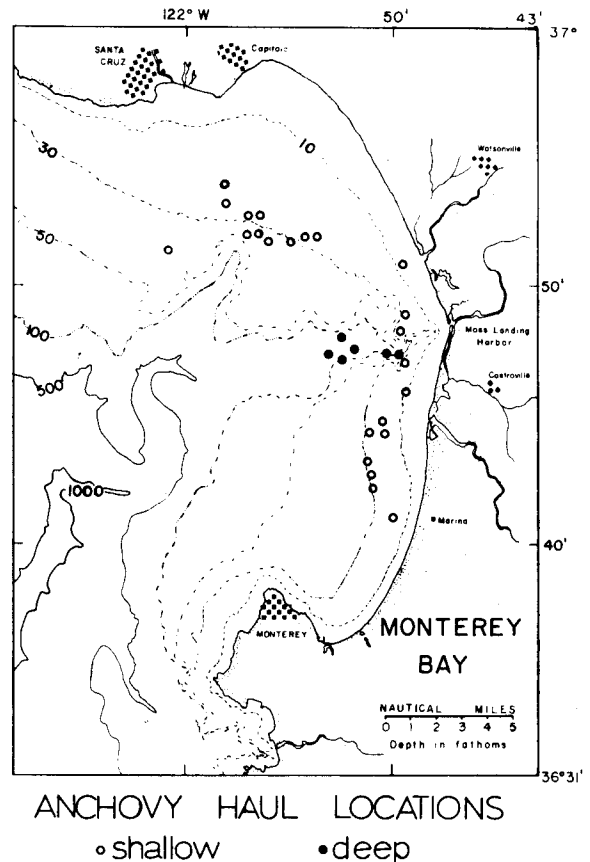

ANCHOVY HAUL LOCATIONS
○ shallow ● deep

Figure 1. Map showing locations of commercial anchovy hauls in Monterey Bay during 1975 and 1976. Dark circles indicate deep samples (more than 64 m) and open circles indicate shallow samples.

In the 29 commercial anchovy haul samples, 19 common taxa were noted, and they were not surprisingly dominated by the northern anchovy, *Engraulis mordax* (Table 1). When ranked by frequency of occurrence, *E. mordax* was followed by the market squid, *Loligo opalescens* (90%), scyphomedusae (76%), *Torpedo californica* (62%), *Citharichthys sordidus* (41%), *Porichthys notatus* (38%), *Genyonemus lineatus* (35%), and *Clupea harengus pallasii* (31%). Other species occurred in trace amounts (see Table 1). When *E. mordax* was included, the percent domination was 99.8%, while without *E. mordax* it was only 59.0%.

Species Composition: Midwater Trawls

During the summer, 27 shallow and 24 deep tows were analyzed that had captured 73,572 individuals and 64,852 individuals, respectively, with a total of 21 common taxa (Figure 3, Table 2). The cumulative number of these taxa for both deep and shallow midwater tows leveled off at around eight to ten tows, with only slight increases continuing to occur, especially for the deep tows (Figure 4). Again, these increases were caused by rare species that occurred only once. The total number of taxa captured in

TABLE 1

**Abundance, Frequency of Occurrence, and Index of Affinity (I) with
Loligo opalescens of Pelagic Organisms Caught in Anchovy Hauls**

	Overall % Frequency	Overall % by Number*	Affinity (*I*) Shallow	Deep
Engraulis mordax...........	100	99.9	0.87	0.61
Loligo opalescens...........	90	76.1	n/a	n/a
Scyphomedusae.............	76	2.9	0.74	0.45
Pelagia sp.	(50)	–	–	–
Chrysaora sp.	(58)	–	–	–
Aurelia sp.	(17)	–	–	–
Torpedo californica	62	0.2	0.76	0.25
Citharichthys sordidus.......	41	1.0	0.58	–
Porichthys notatus	38	6.3	0.61	–
Genyonemus lineatus........	35	0.5	0.58	–
Clupea harengus pallasii	31	8.1	0.43	0.62
Peprilus simillimus	18	0.3	0.38	–
Atherinopsis californiensis ...	17	0.6	0.38	–
Octopus sp.	17	1.8	0.38	–
Cololabis saira	7	0.6	0.20	–
Merluccius productus........	7	0.01	0.20	–
Trachurus symmetricus......	7	0.01	0.20	–
Spirinchus starksi...........	7	2.3	0.20	–
Myliobatis californica	7	0.02	0.20	–
Salps	7	0.01	0.20	–

Total Number Hauls Sampled: 29
Total Tonnage Sampled   557

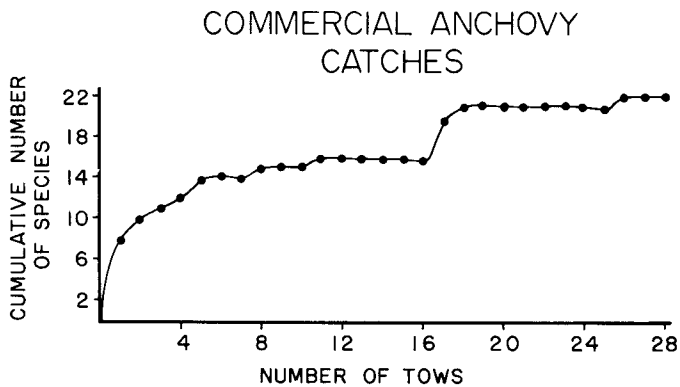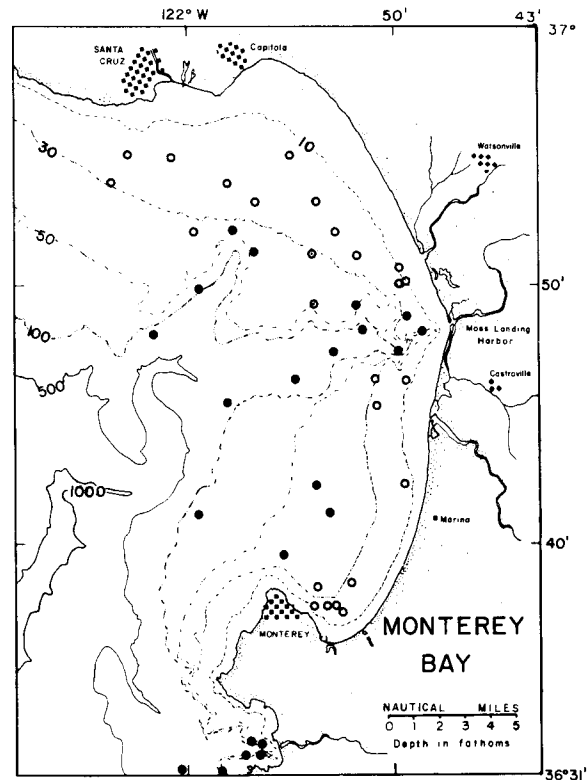*All other species calculated without *Engraulis mordax*.

COMMERCIAL ANCHOVY
CATCHES

Figure 2. The cumulative number of species subsampled from commercial anchovy catches plotted against randomly-ordered number of hauls.

MIDWATER TRAWL LOCATIONS
°summer   •summer
   shallow   deep

Figure 3. Map showing locations of large midwater trawl samples in and around Monterey Bay during summers from 1968 to 1976. Dark circles indicate deep samples (more than 64 m), while open circles indicate shallow tows. The two circles with a dot inside of them represent duplicate locations at both depths.

the shallow tows was 45, while that for the deep tows was 62 (Figure 4). The difference in total taxa was due to an increase in midwater organisms associated with the Monterey Submarine Canyon.

In the 27 summer shallow midwater trawls, 20 common taxa were noted, with the dominance relatively low (34%), shared numerically by *Loligo opalescens*, juvenile *Sebastes* spp., ctenophores, and euphausiids. Other relatively frequent taxa were *Porichthys notatus, Engraulis mordax, Pelagia* sp., *Torpedo californica, Merluccius productus, Peprilus simillimus, Citharichthys sordidus,* and *Clupea harengus pallasii.*

In the 24 summer deep midwater trawls, 21 common

taxa occurred, again with relatively low dominance (46%), led numerically by euphausiids (66%) and followed by *E. mordax, Merluccius productus,* juvenile *Sebastes* spp., *Citharichthys sordidus,* and *Loligo opalescens* (Table 2.) Other species that occurred frequently but not necessarily with high numbers were *Pelagia* sp., *Porichthys notatus,* ctenophores, juvenile *Sebastes paucispinis* and *S. jordani,* and unidentified flatfishes.

The 20 tows taken during the winer produced 2,595 individuals of 19 taxa (Table 3). These tows had a high dominance (56%), led by the northern anchovy, *E. mordax,* with *C. sordidus* and *C. stigmaeus, L. opalescens,* and euphausiids also occurring relatively frequently. The remainder of the total list of taxa closely resembled those caught during the summer, and most of these were low, both in numerical importance and in their frequency of occurrence.

In general, the species composition from the anchovy hauls was quite similar to that found in the large midwater trawl samples. In both, catches were dominated by *E. mordax,* and *L. opalescens,* with other taxa such as

Porichthys notatus, Citharichthys sordidus, and scypho-medusae ranking high (see Tables 1-3). The species similarity index was highest between shallow and deep summer midwater trawl samples (98%). The index was less for the other comparisons, with the summer shallow midwater trawls having an index of 61% with the anchovy hauls and the winter midwater trawls having lower indices when compared with shallow summer midwater trawls (55%), deep summer midwater trawls (54%), and anchovy hauls (52%).

Recurrent Groups

Recurrent group analysis revealed similar groupings of organisms for both methods of sampling. In the shallow anchovy hauls, a major group consisting of *Engraulis mordax, Loligo opalescens, Torpedo californica, Porichthys notatus,* and *Genyonemus lineatus* was resolved (Figure 5). This main group shared affinities with four other taxa, *Citharichthys sordidus* and scyphomedusae (with three out of the five taxonomic pairs having significant indices of affinity), *Clupea harengus pallasii* (with two having significant *I* values) and *Atherinopsis californiensis* (with only a tendency to associate with the taxa
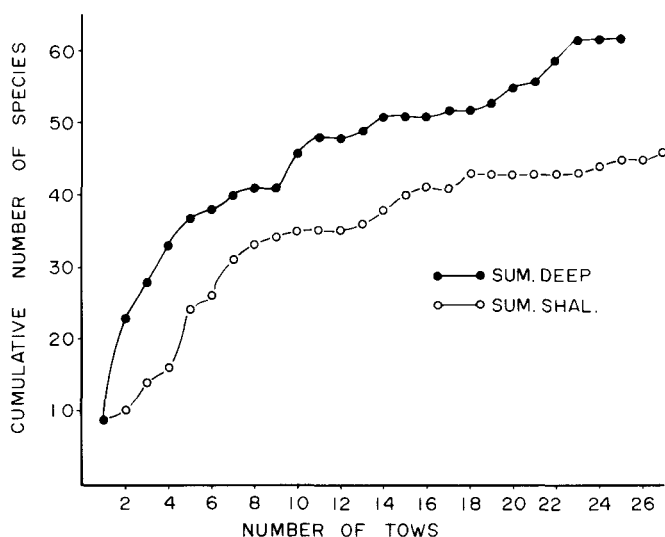

Figure 4. The cumulative number of species caught in large midwater trawl samples plotted against randomly ordered number of tows. The upper curve (dark circles) is for deep (64-91 m) summer tows, while the lower curve (open circles) is for shallow summer tows.

TABLE 2

Abundance, Frequency of Occurrence, and Index of Affinity (*I*) with *Loligo opalescens* of Pelagic Organisms Caught in Summer Midwater Trawls.

	Shallow			Deep		
	% F.O.	% N.	*I*	% F.O.	% N.	*I*
Loligo opalescens	89	11.0	n/a	67	1.0	n/a
Sebastes spp.	63	16.0	0.64	63	6.0	0.33
Porichthys notatus	63	0.01	0.49	42	0.01	0.19
Engraulis mordax	52	6.0	0.61	38	10.0	0.29
Pelagia sp.	52	0.01	0.55	46	0.01	0.33
Torpedo californica	52	0.01	0.66	13	0.01	0.16
Merluccius productus	48	0.01	0.58	54	7.0	0.50
Peprilus simillimus	48	0.01	0.63	17	0.01	0.38
Citharichthys sordidus	37	0.01	0.41	40	2.0	0.25
Clupea harengus pallasii	33	3.0	0.51	8	0.01	–
Ctenophora	30	53.0	0.48	29	0.01	0.25
Sebastes paucispinis	19	0.01	0.35	33	0.01	0.23
Pleuronectiformes	19	0.01	0.35	29	0.01	0.16
Clupeidae	19	0.01	0.26	4	0.01	–
Ophiodon elongatus	19	0.01	0.35	8	0.01	–
Euphausiacea	15	11.0	0.31	29	66.0	0.16
Sebastes jordani	15	4.0	0.31	17	0.01	0.13
Octopoda	15	0.01	0.19	13	0.01	0.31
Citharichthys spp.	15	0.01	0.31	8	0.01	0.23
Leuroglossus stilbius	–	–	–	10	0.01	0.32
Icichthys lockingtoni	4	0.01	–	17	0.01	0.25
Spirinchus starksi	–	–	0.25	–	–	–
Polyorchis sp.	–	–	0.25	–	–	–
Trachurus symmetricus	–	–	0.19	–	–	–
Scyphomedusae	–	–	0.19	–	–	–
Tarletonbeania crenularis	–	–	–	–	–	0.25
Symbolophorus californiensis	–	–	–	–	–	0.23
Parophrys vetulus	–	–	–	–	–	0.23
Total Number Hauls	27			24		
Total Number Individuals	73,572			64,852		

TABLE 3

Abundance, Frequency of Occurrence, and Index of Affinity (*I*) of Pelagic Organisms from Winter Midwater Trawls.

	% F.O.	% N.	*I*
Engraulis mordax	75	74.0	0.47
Citharichthys sordidus	40	2.0	0.12
Citharichthys stigmaeus	35	2.0	0.15
Loligo opalescens	35	1.0	n/a
Euphausiacea	35	1.0	0.27
Porichthys notatus	20	1.0	0.03
Peprilus simillimus	20	1.0	0.00
Torpedo californica	20	0.01	0.38
Ctenophora	20	0.01	0.03
Decapoda	20	0.01	–
Syngnathidae	20	0.01	0.19
Clupea harengus pallasii	15	6.0	0.03
Diaphus theta	15	6.0	–
Chrysaora sp.	15	0.01	0.19
Sebastes sp.	15	0.01	0.08
Salpidae	15	0.01	0.03
Pteropoda	15	0.01	0.03
Thetys vagina	15	0.01	0.03

Total Number Hauls 20
Total Number Individuals 2,595

in the main group; Figure 5). When only deep samples were considered, the three more demersal taxa dropped out leaving only one major group comprised of *E. mordax, L. opalescens,* and *C. harengus pallasii*. Two of these three taxa had a significant index of affinity with scyphomedusae.

The midwater trawls produced similar but more complex recurrent groups (Figure 6). In the 27 shallow tows, two large interconnected recurrent groups emerged, one with *L. opalescens, Clupea harengus pallasii,* and juvenile *Sebastes* spp. included and the other with *Porichthys notatus, Torpedo californica,* and *Pelagia* sp. Five of the nine taxonomic pairs between these two groups had significant indices of affinity. Two additional main groups occurred, one comprised of *Merluccius productus* and *Peprilus simillimus* and the other having only the northern anchovy, *E. mordax.* The first groups had two out of the possible six taxonomic pairs with significant indices of affinity with the two main groups, while *E. mordax* had a significant association with at least one taxon in each of the main groups. Several other groups appeared in these shallow tows. One group was composed of *Sebastes jordani* juveniles, *Octopus* spp., ctenophores, and unidentified flatfishes. Two other taxa had significant affinity with this group, *Ophiodon elongatus* and *Polyorchis* sp. Since these species all had relatively low frequencies of occurrence (Table 2), their significant affinities were based on a low number but a high proportion of co-occurrences, thus placing them in a recurrent group individually that had slight affinity with one of the main groups. Nevertheless, out of 27 tows, they did co-occur sufficiently to warrant separate groups. Another small group consisted of two species of the cephalopod genus *Gonatus,* both too uncommon to appear in Table 2, but having an index of affinity high enough to warrant their assemblage.

In the deep midwater trawls, similar species generally occurred in the recurrent groups (Figure 6), but their positioning differed slightly and association among them was not as evident. One main group was comprised of *Loligo opalescens* and *Merluccius productus;* another of

Citharichthys stigmaeus, Microstomus pacificus, and *Chrysaora* sp.; and a third of *Porichthys notatus, Citharichthys* spp., and juvenile *Sebastes* spp. This third group had an affinity with *Pelagia* sp. One additional group occurred in these samples, comprised of three midwater animals that commonly occupy the Monterey Submarine Canyon (Anderson 1977). These were the zoarcid fish *Lycodapus mandibularis* and the two prawns, *Pasiphaea pacifica* and *Sergestes similis.* Since the tows were taken at night, these species were captured in shallower waters during their nocturnal vertical migrations from the midwater region.

Affinities with Loligo opalescens

During the course of assembling recurrent groups, indices of affinity of the various taxa captured with *Loligo opalescens* were calculated, and these are presented in

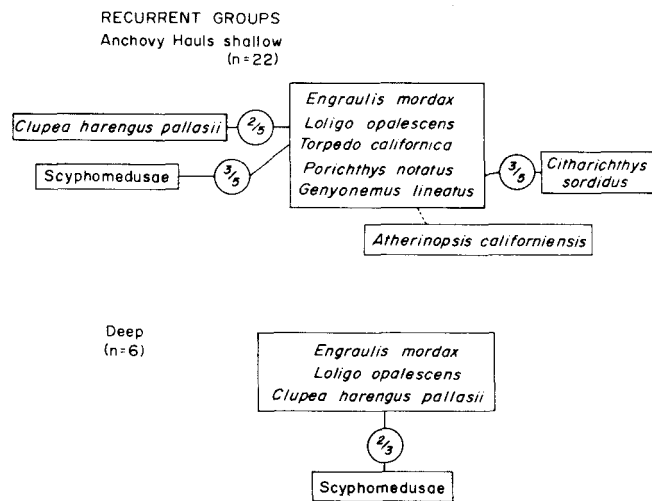Figure 5. Recurrent groups of pelagic organisms taken in 22 shallow (less than 64 m) and 6 deep commercial anchovy hauls in Monterey Bay. Ratios in parentheses indicate the number of significant (i.e. over 0.50) affinities of species between recurrent groups.
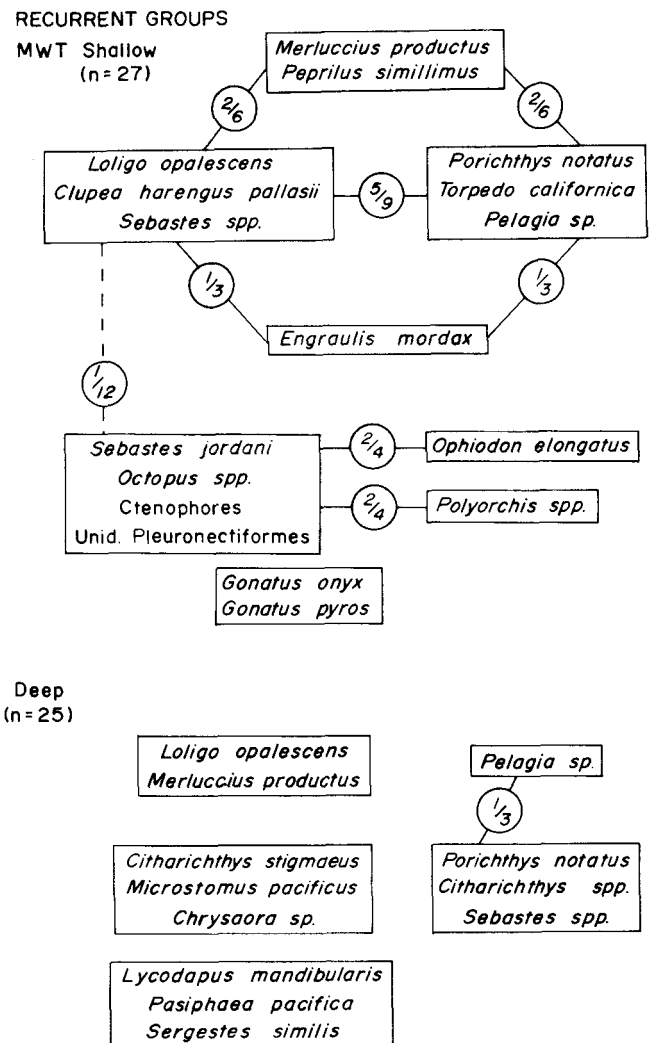
Figure 6. Recurrent groups of pelagic organisms taken in 27 shallow (less than 64 m) and 25 deep (61-91 m) midwater-trawl samples taken in Monterey Bay.

Tables 1, 2, and 3. In the anchovy hauls, those taxa having significant affinity with *L. opalescens* were *Engraulis mordax*, scyphomedusae, *Torpedo californica*, *Citharichthys sordidus*, *Porichthys notatus*, *Genyonemus lineatus*, and *Clupea harengus pallasii* (Table 1). For the summer midwater trawls, all of the above species except *Citharichthys sordidus*, *Genyonemus lineatus*, and *Porichthys notatus* had significant affinities with *Loligo* (Table 2). In addition, juvenile *Sebastes* spp., *Merluccius productus*, and *Peprilus simillimus* were associated with *Loligo* in these trawls. During the winter, none of the taxa captured in midwater trawls had significant affinities with *Loligo*.

DISCUSSION

In evaluating these results, it is essential that we evaluate the applicability of the analytical tools employed. We originally considered using Fager's (1957) recurrent group analysis because we had presence and absence data on our pelagic organisms and because it had been used by several other investigators for such groups as marine phytoplankton (Venrick 1971), marine zooplankton (Fager and McGowan 1963), midwater animals (Ebeling et al. 1970), and demersal fishes (Fager and Longhurst 1968). However, Boesch (1977) recently warned investigators about the value of using recurrent group analysis due to the arbitrary nature of setting the affinity index levels. Since then, a more recent evaluation of the technique by Hayes (1978) indicated that " the index . . . errs on the conservative side and one can put considerable confidence in the reality of recurrent species groups that are derived through its application," especially "if a large number of sites are sampled." Therefore, throughout this discussion, caution should be exercised in interpreting the results due to the nature of the sampling, the application of the recurrent group analysis techniques, and in some cases, due to limited sampling effort.

In general, it appears that recurrent groups of organisms do occur in the pelagic water of Monterey Bay but that they can vary somewhat, depending on location, time of year, and type of gear fished. Nevertheless, the market squid (*Loligo opalescens*) and one of its main associates, the northern anchovy (*Engraulis mordax*), do appear to play a major role in these recurrent assemblages. It is the purpose of this discussion to characterize these assemblages, while interpreting the major differences found among locations, time, and type of gear used. The discussion will center on the predominant species, *L. opalescens*, and will take into account various aspects of the life histories of the associated pelagic and demersal species involved.

In the anchovy haul samples which were dependent on the activity of the fishing fleet, it was not altogether possible to separate seasonal from depth variation. Most of the shallow sets (19 out of 23) were taken in September through October, while the "deep" water samples (over the Monterey Submarine Canyon) were taken in January through March. However, as a first approach to understanding the species associations involved, it is interesting to examine the recurrent groups from these anchovy hauls more closely. Four species associated with *Loligo opalescens* in shallow water do not remain in close association in the samples from deeper water. This could be due to seasonal variation, ability to escape capture by swimming downward in deep water before the purse seine is closed, or simply due to the fact that they do not occur over deep water. We do not believe that this resulted from seasonal variation, since all four species either occurred in the midwater trawl samples over the year or were present in bottom trawls that are taken intermittently throughout the year (Cailliet, unpublished data). The second and third possibilities are certainly to be considered. Anchovy nets are more effective in capturing northern anchovies in shallow water of 30 fathoms or less (Messersmith 1969), where they are able to touch bottom and prevent fish from swimming out from under them. Therefore, this possibility could affect the capture of such demersal fishes as *Citharichthys sordidus*, *Genyonemus lineatus*, and *Porichthys notatus*. The third possibility that these fish do not occur over deep water needs to be examined more carefully for the four species under consideration. Both *Torpedo californica* and *P. notatus* occurred frequently and showed numerous significant joint occurrences with other species in the shallow midwater trawls. However, only *P. notatus* retained high frequencies and significant joint occurrences in the deep midwater trawls. It appears, then, that *T. californica* is restricted to more inshore areas, at least in midwater at night, whereas *P. notatus* can occur over deep water at least during the summer months. Indeed, a recent paper by Bray and Hixon (1978) found that adult *T. Californica*, which usually are not seen during the day in nearshore kelp beds off southern California, are very active preying on fishes in the midwater off these kelp beds at night. In addition, our data corroborate earlier reports that *P. notatus* is a vertical migrator, moving off the bottom in search of prey at night (Lavenberg and Fitch 1966; Hart 1973). Our lack of spring samples precludes investigating its documented migration inshore during spring and early summer to spawn in shallow water (Fitch and Lavenberg 1971). *Citharichthys sordidus*, a very common demersal flatfish, cannot be excluded from the deep midwater areas. It showed high frequencies of occurrence in all comparisons except the deep-water anchovy hauls. However, *C. sordidus* showed the lowest percent by number and no significant joint occurrences in the shallow summer midwater trawls, suggesting that it may only leave the bottom near canyons or

deep-water areas. Stomach-content analyses of this species (Cailliet,unpublished data) indicate that it commonly feeds on nektonic organisms such as euphausiids, especially near the edge of the Monterey Submarine Canyon. Therefore, it either comes off the bottom to feed on these pelagic organisms or the prey come very close to the bottom during the downward portion of their vertical migration pattern. In contrast to the above three species, *Genyonemus lineatus* was markedly absent from all midwater trawl samples. Since *G. lineatus* is usually caught in water shallower than 100 feet (Frey 1971), they probably occurred in the shallow-water anchovy hauls because the seines scraped the bottom and were effective at catching them.

The other associates of *Loligo opalescens*, especially those such as *Clupea harengus pallasi* and scyphomedusae which occurred in anchovy haul samples in shallow and deep water, are more pelagic in habit and probably do regularly contribute to the pelagic assemblages in the area. Both associates also occurred in recurrent groups from the midwater trawl samples. The occurrence of *Atherinopsis californiensis* in the shallow anchovy haul recurrent groups may be an artifact of sampling, since that was the only time that they were significantly associated with any of the pelagic organisms under consideration.

The strong association between *Loligo opalescens* and *Engraulis mordax* in the anchovy hauls does not appear as strong in summer or winter midwater trawl catch analysis. Here, although both species appear commonly, they do not occur in the same recurrent groups during the summer, with *L. opalescens* associating more with *Clupea harengus pallasii*, juvenile *Sebastes* spp., and *Merluccius productus*. Indeed, in the winter midwater trawls, which were a combination of an equal number of deep and shallow trawls that had to be lumped due to poor cumulative species plots and small sample size, *L. opalescens* lacked significant associate species and had a low frequency of occurrence and relative abundance. This can be explained either by sampling strategy, the unavailability of squid in large numbers during the winter survey, or low availability in midwater of squid associated more with the bottom during these months. Certainly, sampling strategy could be a factor, since the winter CDFG Sea Survey cruises were primarily after anchovies, but if *L. opalescens* truly is an associate of *E. mordax*, it would have shown up more convincingly. Studies on another loliginid squid, *L. pealei*, indicate that they are vertical migrators, moving off the bottom at night during winter months (Roper and Young 1975). If *L. opalescens* behave in this fashion, they should have been in the water column during these trawls, yet they were not that commonly caught. Commercial landings of squid in Monterey Bay, during the winter months under consideration, may reflect availability (Fields 1965). During the two months of the midwater trawl survey (February 1968 and October 1969), squid landings in Monterey Bay were almost nonexistent (Heimann and Carlisle 1970; Pinkas 1970). In light of this, it would seem likely that during these months *L. opalescens* was simply not available in the bay to this kind of fishing gear. Perhaps squid are simply so randomly dispersed during the winter months that they are unavailable in large numbers to midwater trawls. The lack of associate species, other than *M. productus* in the deep summer trawls where *L. opalescens* was still abundant and frequently occurring, suggests a more random dispersion of other organisms captured in these trawls in relation to *L. opalescens*, thus making their co-occurrence less likely.

Obviously, since the anchovy hauls were seeking anchovies, these fish co-occur with every other species, oftentimes significantly. However, in the more randomly scheduled midwater trawls during the summer months, there was no target species, and perhaps a clearer picture of the relationship between squid and their closest associate, *Engraulis mordax*, may result. Since these two species were only associated in shallow summer trawls, association in deeper waters is perhaps not strong. In addition, using the numerous, more random, summer midwater trawl samples, a clearer picture of the association between *Loligo opalescens* and its other associates is possible. In the shallow summer hauls, associates with significant indices of affinity were numerous, including *Clupea harengus pallasii* and *Sebastes* spp. (which were both in the same recurrent group as *L. opalescens*, *Merluccius productus*, and *Peprilus simillimus* [in a closely-related group]), *Porichthys notatus*, *Torpedo californica*, and *Pelagia colorata* (in another closely-related group) and *E. mordax* (by itself; Figure 6).

Miller and Schmidtke (1956) reported that *Clupea harengus pallasii* is not abundant in Monterey Bay during April through November; this is reflected in our results by an increased frequency of occurrence during summer months, at least in the shallow samples. Since they occurred much less frequently in the summer deep tows, it suggests a more inshore, shallow distribution for herring. *Peprilus simillimus* occurred only in the shallow-water anchovy hauls and midwater trawls, closely agreeing with the published information on this species (Fitch and Lavenberg 1971). It is difficult to explain the association between *P. simillimus* and *Merluccius productus* during the summer months, except that they both feed upon planktonic organisms. Large numbers of juvenile rockfishes were taken in the summer midwater trawls, ranging from 39 to 65 mm standard length in the shallow-water stations to 76 to 153 mm standard length in the deep samples. As many as 10,000 individuals were taken in a single haul, with larger numbers caught nearer the kelp bed areas. The pronounced absence of these juve-

niles from the anchovy commercial hauls can be simply explained by a lack of samples from near kelp bed areas. Miller and Geibel (1973) found, in a study of juvenile rockfish in the Monterey Bay area, that "concentrations of these fish appeared in April and May each year and remained densely aggregated in the kelp bed areas ...." This implies that juvenile rockfishes occur in these trawls seasonally and, therefore, only became pelagic associates with these other organisms during their juvenile stages.

Adult *Merluccius productus* were reported by Alverson and Larkin (1969) to undergo northward and inshore summer migrations. They also reported acoustic results indicating that this species undergoes a diel vertical migration paralleling the vertical migration pattern of the euphausiid, *Thysanoessa spinifera*. Alton and Nelson (1970) showed that the vertically migrating euphausiids *T. spinifera* and *Euphausia pacifica* were the leading food of *M. productus* both in frequency of occurrence and by weight, off Washington and Oregon. In Monterey Bay, it appears that the same is true (G.V. Morejohn, personal communication). Coincidentally, Karpov and Cailliet (in press) have shown that these two species of euphausiids dominated the diet of *Loligo opalescens* taken in the Monterey Bay area. When this information is combined with the fact that *Loligo opalescens* and *M. productus* were the only two species to remain associated in both the shallow and deep summer midwater trawls, it suggests that this association reflects utilization, perhaps competition, for the same resource. Certainly, this is conjectural, since euphausiids could not be included in the recurrent group analysis due to the mesh size; nor were stomach contents analyzed in all of these samples. However, this association warrants further investigation. Additionally, Karpov and Cailliet (1978) reported that peak feeding *L. opalescens* during summer months is at midday, while Alton and Nelson (1970) suggested that peak feeding in *M. productus* occurred during night hours.

While this analysis of recurrent groups of pelagic organisms from Monterey Bay has certain limitations, it does point out certain associations among organisms and suggests reasons for these associations. The primary organizing factor could be food source. The main members of recurrent groups in the pelagic waters of Monterey Bay, whether determined by commercial anchovy haul or winter and summer midwater samples, tend to feed upon the same kind of macroplankton euphausiids (G.V. Morejohn, personal communication). This euphausiids "link" may well be the reason that species such as *Loligo opalescens, Merluccius productus, Porichthys notatus, Clupea harengus pallasii,* juvenile rockishes (*Sebastes* spp.), *Peprilus simillimus, Citharichthys stigmaeus,* and *C. sordidus* variously come out

in recurrent groups together. The association of these species with the northern anchovy, *Engraulis mordax,* is not quite as easy to explain. However, since *E. mordax* feeds on microplankton that live in the same general area of the pelagic ecosystem, it is not unreasonable to expect them to co-occur with such predatory organisms as squid. Indeed, young anchovies probably contribute to at least a portion of the diet of larger squid (Karpov and Cailliet, in press) .Despite the major problems inherent in trawling studies and in recurrent group analysis, there appears to be ample evidence that recurrent assemblages of pelagic species do occur in Monterey Bay waters and that both *L. opalescens* and *E. mordax* play very important roles in influencing the nature of these assemblages.

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DISTRIBUTION OF LARVAL SQUID, *LOLIGO OPALESCENS,*
IN VARIOUS NEARSHORE LOCATIONS

CONRAD W. RECKSIEK AND JERRY KASHIWADA
Moss Landing Marine Laboratories
P.O. BOX 223, Moss Landing, CA 95039

ABSTRACT

Three distinct sampling efforts employing different plankton-collecting gears aimed at collecting California market squid, *Loligo opalescens,* in nearshore waters from San Diego to Monterey Bay are described. Larval *Loligo opalescens* occurrence in the hauls was low and patchy, corroborating the experience of past workers. Over the Monterey spawning grounds, the use of a specially designed bottom-fishing plankton net was found to be more generally effective than the other gears.

INTRODUCTION

The early life history of *Loligo opalescens* is unclear. Fields (1965) suggests that the newly hatched larvae may be carried long distances by coastal currents. McGowan (1954), from 10-minute tows with a 0.40-m net in the vicinity of La Jolla, California, encountered few larval squid, even though the area harbored considerable quantities of hatching egg capsules. He concluded that the larvae were swept away by currents. Okutani and McGowan (1969) in their studies of CalCOFI samples collected 1954-1957 encountered *Loligo opalescens* (3.5 to 7 mm dorsal mantle length) at only 93 of 2,029 inshore stations (1,193 individuals). Offshore stations yielded 42 individuals from 1,866 tows.

The abundance of *L. opalescens,* though ranked third relative to other squid species, was less than 1% of northern anchovy, *Engraulis mordax,* larvae. Okutani and McGowan (1969) state that the CalCOFI plankton-sampling scheme may have been inadequate for estimating absolute abundance of larval *L. opalescens*. By contrast, Mais (1974), reporting the results of pelagic fish surveys (1966-1973), using midwater-trawl gear, found juvenile and adult *L. opalescens* in 36.3% of 1,375 tows. The apparent scarcity of larval *L. opalescens* in plankton hauls is surprising considering an apparent high juvenile-adult biomass (Gulland 1971; Baxter et al. 1968; Voss 1973; Mais 1974). This paper describes our progress in determining distribution patterns of *L. opalescens* larvae in an attempt to understand the scarcity of larvae and post-larvae in standard plankton samples.

METHODS AND MATERIALS

Several distinct gear types were used in collecting larval *L. opalescens*. In Monterey Bay (Figure 1, inset), an opening-closing net with a square-mouth (1.8-m) opening, as described by Hopkins et al. (1973), was used in an attempt to delimit vertical distribution. Depths were estimated using an inclinometer and metered block. Mesh size decreased from about 6 mm at the mouth to a cod-end liner of 1 mm. This gear was fished from Moss Landing Marine Laboratories research vessels *Artemia* and *Oconostota.*

Nearshore oblique tows in the upper 100 m were taken from San Diego to Morro Bay (Figure 1) in an attempt to define geographical concentrations of larvae. These tows were made with a continuously open net similar in design to that used in Monterey Bay but with slightly larger mesh. In the case of operation in shallow water, the maximum safe operation depth was shifted upward. In general, the net was allowed no lower than about 25 m from the bottom. Mesh sizes decreased from 9 mm to a cod-end liner of 1 mm. The tows were taken from the California Department of Fish and Game research vessel *Alaska* (Cruise 76A4).

Larval squid were also collected over the traditional spawning grounds near Monterey (Figure 1, inset) adjacent to the bottom by mounting a standard 0.5-m plankton net to a specially designed frame fitted with sled-like runners. This device enabled fishing the net in such a way that the lower rim was approximately 10 cm off the substrate surface. It was used in shallow (20-30 m) water. Tows in which egg cases were caught on the sled were not included with the data presented, since it could not be determined if squid hatched during the process of capture. A midwater comparison sample was obtained by fastening a 0.5-m plankton net to the wire. A rough calculation based on wire angles was used to place the comparison plankton net at mid-depth. The research vessel *Tage* of Hopkins Marine Station was used to deploy this gear.

The squid captured by the various gear were measured from the posterior to the anterior ends of the mantle on the dorsal side (dorsal mantle length). Squid caught on the spawning grounds near Monterey were dissected to determine if the squid were feeding.

RESULTS AND DISCUSSION

Our initial purpose in studying larval squid was to describe patterns of spatial distribution. We were interested in ascertaining the feasibility of using larval squid abundance as an index of recruitment. Initially, it was decided that a relatively fast-moving plankton sampler was required in order to increase fishing success over the 1-m CalCOFI net, as reported by Okutani and McGowan (1969). We presumed that avoidance of the CalCOFI
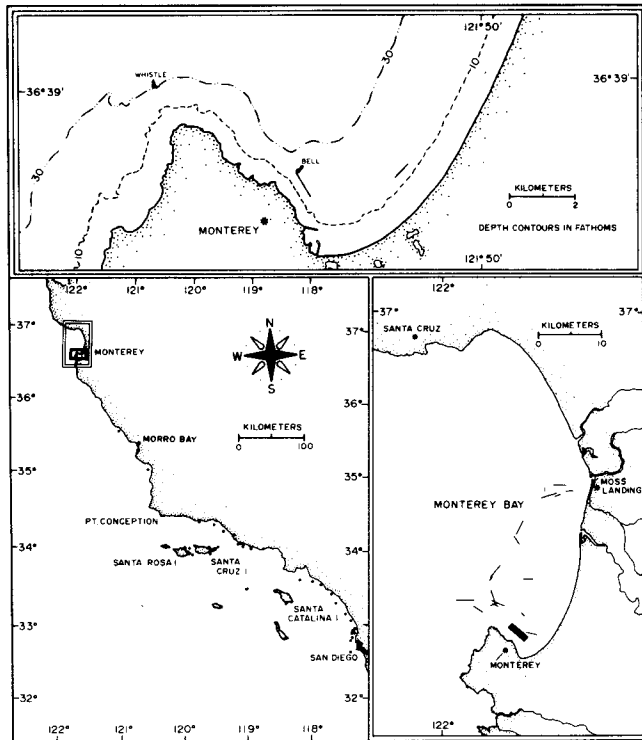
Figure 1. Sampling locations for three methods of collecting larval *Loligo opalescens*. Central figure: 1.8-m square-mouth trawl, open oblique tow, 30 May 1976 to 14 June 1976; inset: Monterey Bay, opening-closing 1.8-m square-mouth trawl, 15 September 1975 to 10 March 1976; inset: South Monterey Bay, bottom and midwater 0.5-m nets, 21 July 1976 to 31 August 1976.

TABLE 1

Larval *Loligo opalescens* Collected with Three Distinct Sampling Strategies and Locations in Monterey Bay and Nearshore Waters between La Jolla and Morro Bay, California.

	Opening-Closing 1.8-m Square-Mouth Trawl, South-Central Monterey Bay, 15 September 1975 to 10 March 1976	Open Oblique Tow 1.8-m Square-Mouth Trawl, La Jolla to Morro Bay, 30 May 1976 to 14 June 1976	Bottom and Midwater 0.5-m Plankton Nets, South Monterey Bay, 21 July 1976 to 31 August 1976
Number stations ...	29	30	29
Number positive stations	13	6	20
Range trawl time (min)	10-30	9-18	8-12
Total number squid.............	58	52	320
Range squid/tow...	0-11	0-34	0-113
Mean squid/tow ...	2.00	1.73	6.83
Coefficient of variation squid/tow.........	156	374	217
Mean dorsal mantle length (mm)	3.45	8.22	2.10
95% confidence interval of mean dorsal mantle length (mm)	3.1-3.8	7.35-9.09	2.07-2.13

net was responsible for poor fishing success.

In an effort to delimit patterns of vertical distribution, 29 trawls of 10- to 30-minutes duration, day and night, using the opening-closing net, were accomplished September 1975 through March 1976 at various stations in southern Monterey Bay and over the axis of the Monterey Submarine Canyon. An attempt was made to corroborate Okutani and McGowan's (1969) inference that the larvae could be expected in the 25- to 40-m stratum. Of 29 trawls, 14 occupied that layer. The two most successful tows contained 9 and 11 squid. These were encountered at 40 m and 30 m, respectively.

Only 58 larvae, an average of 2 squid/tow, were collected (Table 1). Since the small size of the samples did not appear to justify the data-gathering effort, we decided to attempt locating concentrations of animals before investigating further the problem of favored strata. We therefore planned to use similar gear but over a much more extensive area and throughout the upper 100 m.

For thirty tows at various nearshore stations (depths generally shallower than 200 m, except over submarine canyons or escarpments), an average of 1.77 squid/tow was collected (Table 1). These tows were accomplished at night, late May to mid-June 1976. Of the thirty tows

ranging in duration from 9 to 18 minutes, two contained 88% of the squid: 12 and 34 animals. Midway through the cruise, it was decided that the low fishing success did not warrant further effort.

Our results thus far paralleled the experience of others: larval *Loligo opalescens* occurrence in the samples was low and patchy. It appeared that the larvae were either demersal or were elsewhere, perhaps in deep water. To test the former hypothesis, we began fishing 0.5-m plankton nets close to the bottom on the squid spawning grounds off the City of Monterey (described in Fields 1965; Figure 1, inset). The results (Table 1) thus far, 21 July to 31 August 1976, indicate a higher fishing success than with the other gears. Samples from the bottom net

TABLE 2

Bottom (30 m) and Mid-Depth (15 m) Larval Squid Catch from 0.5-m Plankton Nets Near Squid Spawning Grounds, Monterey, California.

	Bottom		Midwater	
Date (1976)	Tows	Total No.	Tows	Total No.
21 July....................	2	49	–	–
27 July....................	3	25	2	7
3 August...................	4	181	4	45
10 August	2	0	2	5
17 August	4	3	4	4
31 August	1	1	1	0
Total	16	259	13	61
Catch/Tow................	16.2		4.7	

have been most encouraging (Table 2) with catch/tow averaging 16.2 in contrast to a midwater mean of 4.7.

One possible explanation for the high catches with the bottom net is that the sled caused eggs to hatch by disturbing them. LaRoe (1971) found that large numbers of the squid *Sepioteuthis sepioidea* hatched following mechanical agitation. This is probably not the case, since on some occasions, squid egg cases were caught on the runners of the sled or in the cod end of the net and the data from such catches were not used. If the sled moved through the egg-case clusters, there would probably be some egg cases on the sled. Many of the most successful tows with the sled had no traces of egg cases.

One interesting result of comparisons with midwater and bottom plankton tows was an increase in catch in the midwater net and a concurrent decrease in the catch in the bottom net as daylight increased (Table 3). This observation might be explained by observations on the behavior of newly hatched squid. Fields (1965) found that squid usually hatch during the night and that they are positively phototactic. Squid hatching at night on the spawning grounds would tend to stay near the bottom where they would be vulnerable to the bottom net. After sunrise, the squid would be attracted to the light at the surface and would be more vulnerable to the midwater net.

It is difficult to make comparisons between the three differing collecting techniques. Since we have no estimates of the volume of water filtered by the nets and the nets were towed at different speeds, comparisons cannot be made of the success of capture/volume filtered, nor the success/minute towed.

One of the new methods of comparison available from our data, the means and confidence limits on the means of dorsal length are, perhaps, the best. These comparisons show that different nets sampled different sizes of squid (Table 1). Since mesh size differed, one explana-

tion for the differences observed is that smaller squid escaped the net with larger mesh. The contrasting catches might also be explained by the locations in which the nets were fished. Nets that sampled away from the spawning grounds probably would be expected to catch larger animals, since some growth would occur during the movement off the spawning grounds.

Although quantitative comparisons cannot be made, we believe that the relatively high catches with the plankton net towed near the bottom are significant. Since these tows were relatively short (8-12 minutes) and the mouth of the net is much smaller than the nets used previously, the amount of water filtered was much less; the high catches are, therefore, even more pronounced.

Since little variability was noted in the squid caught and all squid examined had large yolk sacs, apparently the animals do not remain on the spawning grounds for a long time or else, presumably, we would have encountered more developed stages. One would expect that catching newly hatched squid on spawning grounds would be fairly simple, yet McGowan (1954) found difficulty in catching them in an area covered with egg capsules. The success of the sled in capturing young *Loligo opalescens* is surprising in the light of past experience (McGowan 1954; Okutani and McGowan 1969).

TABLE 3

Daylight and Dark Bottom (30 m) and Mid-depth (15 m)
Larval Squid Catch from 0.5-m Plankton Nets Near
Squid Spawning Grounds, Monterey, California

Date (1976)	Light Condition	Bottom Squid Catch	Midwater Squid Catch
21 July		–	–
27 July		–	–
3 August		113	7
10 August	Full Darkness	0	1
17 August		1	1
31 August		1	0
21 July..........		49	–
27 July		25	7
3 August	Daylight	68	38
10 August		0	4
17 August		2	3
31 August		–	–

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INDICES OF THE AVAILABILITY OF MARKET SQUID, LOLIGO OPALESCENS, TO THE MONTEREY BAY FISHERY

JAMES E. HARDWICK AND JEROME D. SPRATT
Operations Research Branch
California Department of Fish and Game
2201 Garden Rd.
Monterey, CA 93940

ABSTRACT

The availability of market squid to the Monterey lampara fleet has fluctuated grossly in the past two decades, causing considerable economic hardship in recent years. Fishermen and scientists have since 1970 become increasingly curious about the cause of these fluctuations in squid availability. The authors have shown squid to be relatively unavailable to the Monterey fishery in 1952, 1958, 1960, 1961, 1966, 1970, 1973, and 1975. Several indices of the availability of squid to the Monterey fishery suggest an inverse relationship between squid availability and the previous fourth-quarter sea elevation.

INTRODUCTION

The Monterey market squid fishery is one of California's oldest fisheries. About 113 years ago Chinese immigrants began fishing for squid in Monterey Bay with small hand-hauled purse seines. In 1905 Italians introduced the lampara net, which is still in use today. Squid were dried for shipment to the Orient in the early years of the fishery. Canning and freezing began in the early 1920's (Scofield 1924; Classic 1929). Catch records date back to 1916, and prior to 1943 the annual Monterey squid catch averaged 2.4 million pounds. During and immediately after World War II, Monterey landings increased to an average of 17.8 million pounds/year. The principal use of this squid was for export under the Marshall Plan. Landings dropped after 1948, but the large exports from 1943 to 1948 established a considerable market for canned squid. The export of canned squid and the increased demand for frozen squid since 1960 accounts for the bulk of the present fishery. Annual landings at Monterey from 1950 to 1975 have averaged 9.1 million pounds. The peak year was 1956 when 19.6 million pounds were landed, and the worst year was 1973 when 1.2 million pounds were landed.

Since 1960, the squid fishery in southern California has been competing with the Monterey Bay fishery and now accounts for over 50% of the statewide catch.

An attempt to identify the years of poor squid availability to the Monterey fishery and a search for a hypothesis to explain these changes in availability are presented in this paper. A look at Monterey squid landings reveals several years in the past three decades when landings were exceptionally low.

It has been reported as recently as 1972 (Crooke) and 1974 (Norberg) that fluctuations in squid catches are primarily a result of changing canners' demand. This statement may hold true for southern California squid landings, but those close to the Monterey fishery know very well that fluctuations in the Monterey squid landings since 1969 have been due to the changing availability of squid to the fishermen, not due to fluctuations in demand.

Fishermen at Monterey in 1970 were being offered as much as ever for their squid, but landings remained low and fishermen and dealers alike were demanding an investigation by scientists. The senior author set out in July of that year to discover whether the poor availability of squid in Monterey that summer was a new occurrence or whether a similar situation had occurred previously.

INDICES OF AVAILABILITY

Annual Monterey Catch

Catch may be a good indicator of availability of squid to the fishery in years where landings are extremely high or low. The catch may not give an indication of availability in near-average years. Availability could be high but landings depressed because of lack of demand. Availability could also be low and landings good because of increased fishing effort. The annual Monterey landings indicate that 1949, 1950, 1952-53, 1958, 1960-61, 1967, 1970, 1973, and 1975 were years of poor availability (Figure 1).
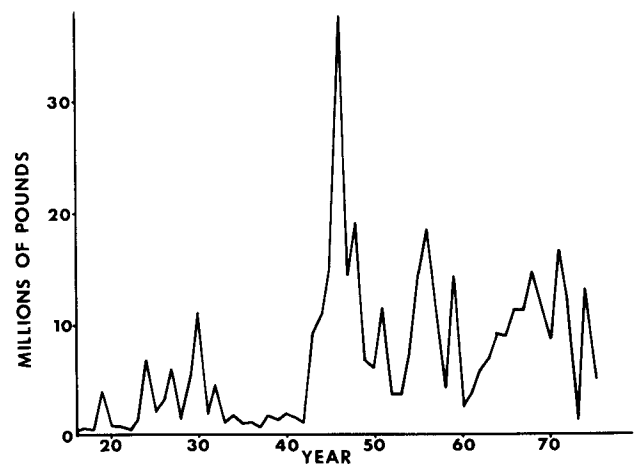

Figure 1. Monterey squid landings, 1916-76.

Catch Per Delivery Day

The best measure of the availability of fish to the fishery is catch per unit of effort. The squid fishermen at Monterey have never filled out daily activity logs, and data are not available to calculate total fishing effort. We do have records of daily landings by boat since 1960, but this includes only boats that were successful in catching squid. When the availability of squid is poor, even successful boats can be expected to reflect this with poor catches. The annual landings at Monterey were divided by the number of boat delivery days. The average catch per delivery day is higher than it should be because unsuccessful boats are not included. When availability is good, limits are placed on boats by fish buyers, which tends to depress the catch per delivery day. Catch per delivery day is a better indicator of poor availability than good availability.

Monterey squid fishermen have fished for squid every summer since 1950. Their success reaches its peak in May, June, and July. They become very upset if they cannot catch squid in these months. Years of low catch per delivery day were 1960, 1961, 1970, 1973, and 1975 (Figure 2). Early catches during the 1976 season indicate this will also be a poor year.

Price Paid to Fishermen and the Percent Canned

The price paid to fishermen varies indirectly with availability of squid to the Monterey fishery. The price for squid is negotiated before the fishing season begins—before it is known how available squid will be to the fishery—and price does not change during the season.

The reason the mean annual price paid to fishermen is high when availability is poor can be seen when the uses for squid are examined. Squid sold to fresh fish markets and squid sold for freezing purposes command two to three times the price of squid sold to canneries for canning. Fishermen sell all they can at the higher fresh and freezing prices before selling any squid to the canneries. Thus, in years of poor availability, nearly all squid is sold at the higher fresh and freezing prices, which raises the mean annual price paid to fishermen. In good years the mean annual price is usually lowered because canneries buy more squid at the lower canning price. This is the mechanism that has resulted in an increase in the price paid to fishermen when landings are poor.

Increases in mean annual prices paid to fishermen have occurred in 1952, 1956, 1958, 1960 and 1961, 1963 and 1964, 1966, 1969 and 1970, 1972 and 1973 (Figure 3), and few squid were canned in 1952, 1960, 1961, 1970 and 1973 (Figure 4). However, price increases and reduced canning are not enough to indicate poor availability since a reduced demand for canned squid would also cause increases in the mean annual price paid to fishermen. Some indices other than price fluctuation and volume of squid canned are necessary to measure the availability of squid to the fishery.
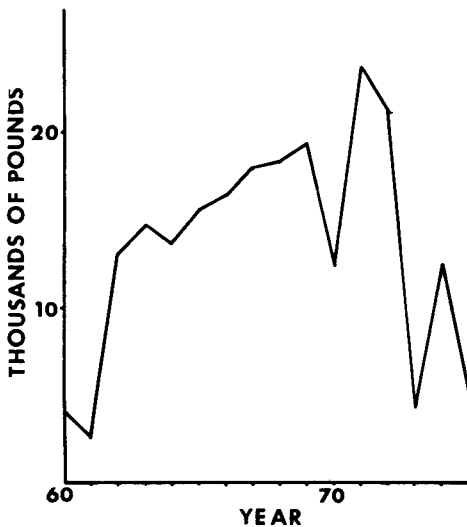

Figure 2. Monterey squid landings per delivery day, 1960-75.

We must look to less precise measures of availability for the years prior to 1960, as the data have not been stored in a manner that will permit retrieval of catch-per-delivery-day data.
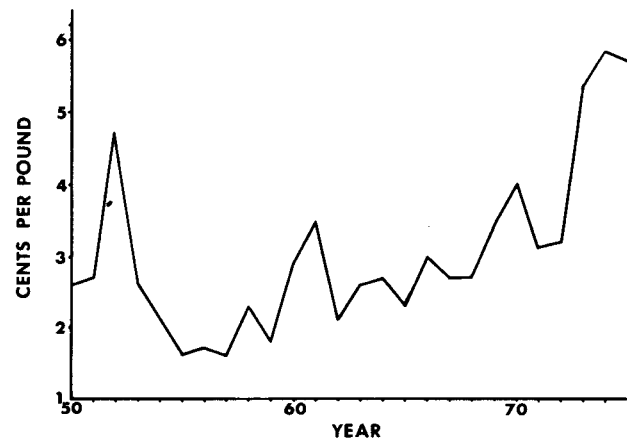

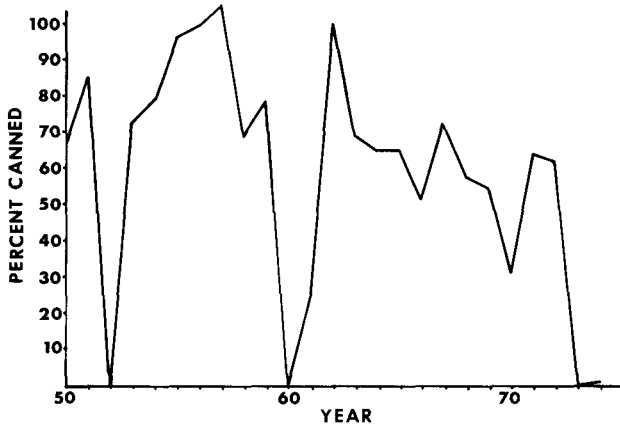Figure 3. Mean annual price paid to Monterey fishermen for squid, 1950-75.

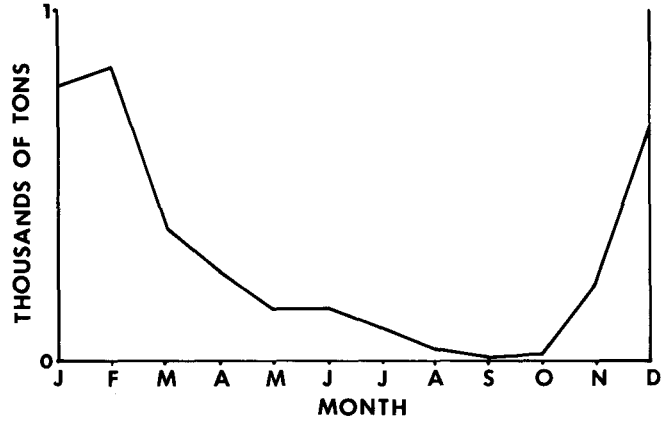Figure 4. The percent of Monterey squid landings canned, 1950-75.

Figure 6. Southern California mean monthly squid landings, 1955-74.

Ratio of Monterey to Southern California Landings

Squid are usually most available to Monterey fishermen from May through July (Figure 5). They are most available to southern California fishermen from December through February (Figure 6). The Monterey fishery is much older than the southern California fishery, and dealers and brokers have traditionally tried to fill orders for squid with landings from Monterey. They fill orders with southern California squid when they are unable to fill them with Monterey squid. Poor Monterey landings are usually followed six months later by good southern California landings. The seasonal landings at Monterey compared with the following seasonal landings in southern California should be an index of the availability of squid to the Monterey fishery (Figure 7). High landings in southern California following poor squid landings at Monterey would be expected to indicate poor availability at Monterey.

One problem with this index is that once dealers and brokers have found a source of squid in southern Cali-

Figure 7. The ratio of southern California November-March squid landings to the previous northern California April-August landings.

fornia they may return to that source to fill future orders rather than going back to the Monterey sources, resulting in reduced demand at Monterey for several years following a year of squid unavailability. Therefore, a sharp decline in this availability index is a better indicator of the unavailability of squid at Monterey than a continuing low index. Squid were very likely unavailable to fishermen at Monterey in 1952, 1958, 1960, 1961, possibly 1964 and 1966, 1970, 1973, 1974, and 1975. We know from personal experience with the fishery at Monterey that fishermen had difficulty finding squid in 1970, 1973, and 1975.

DISCUSSION

The junior author has combined four indices of availability into a single index (Figure 8). The four indices are annual Monterey landings, ratio of Monterey to southern California landings, catch per delivery day, and price paid to fishermen. Each year is a numerical value equivalent to the number of indices indicating poor squid availability to the Monterey fishermen. The maximum pos-

Figure 5. Monterey mean monthly squid landings, 1955-74.

sible value for the years 1950 to 1959 is 3 as catch-per-unit-of-effort data are unavailable for those years. The maximum value possible for the years 1960 to 1975 is 4. This index indicates that 1952, 1958, 1960, 1961, 1966, 1970, 1973, and 1975 were years of poor squid availability to the Monterey fishery (Table 1).

Monterey landings were poor in 1950. The southern California landings were also poor, and the price paid to fishermen did not change from 1949. Lack of demand caused by large inventories of squid that remained from the good years of 1946-48 very likely suppressed the catch at Monterey. If poor availability at Monterey was the reason for poor catches, the southern California catch would have increased.

Figure 8. The number of indices indicating poor availability of squid to the Monterey Bay fishery and the Avila fourth-quarter sea-level anomalies.

The next year of poor catch at Monterey was 1952. The price increased at Monterey, and the southern California catch also increased. All three indices indicate squid were not available at Monterey in 1952.
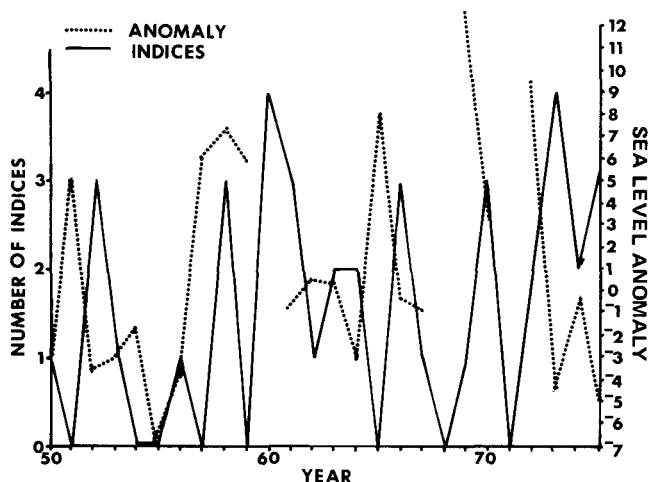
In 1953 the Monterey squid catch was again poor, but southern California landings also dropped from 1952. The price also dropped during 1953, indicating that lack of demand was an important factor in 1953.

From 1954 to 1957, catches were good and prices were stable, indicating good availabilty.

Catches dropped during 1958 at Monterey and triggered inceased catches in southern California. The price also increased in 1958 and all three indices indicate that poor availability caused the poor catches at Monterey.

The 1960 catch was the lowest at Monterey since 1942. All indices indicate that poor availability was the cause. These same conditions prevailed in 1961; the catch was low, southern California landings increased,

TABLE 1.

Indices of the Availabiliy of Squid to the Monterey Bay Fishery

Year	Pounds landed	May-July lbs/delivery	¢/lb	Percent canned	S. Cal. Nov-Mar N. Cal. Apr-Aug	No. of indices*
1950	5,922,571		2.6	67	0.00	1
1951	11,632,468		2.7	86	0.00	0
1952	3,545,653		4.7	0	2.50	3
1953	3,526,829		2.6	73	0.26	1
1954	7,477,922		2.1	79	0.02	0
1955	14,120,513		1.6	97	0.02	0
1956	18,594,241		1.7	100	0.02	1
1957	11,956,541		1.6	105	0.34	0
1058	3,902,936		2.3	69	1.59	3
1059	14,252,042		1.8	89	0.01	0
1960	2,235,935	4,069	2.9	0	1.03	4
1961	3,686,284	2,601	3.5	25	3.78	3
1962	5,652,857	13,100	2.1	100	0.83	1
1963	6,754,463	14,831	2.6	69	0.72	2
1964	9,101,623	13,777	2.7	65	1.15	2
1965	8,865,195	15,580	2.3	65	0.89	0
1966	11,207,349	16,423	3.0	52	1.06	3
1967	11,233,271	17,849	2.7	73	0.94	1
1968	14,578,281	18,445	2.7	58	0.47	0
1969	11,560,220	19,396	3.4	55	0.96	1
1970	8,627,115	12,455	4.0	31	3.26	3
1971	16,646,620	23,749	3.1	64	0.50	0
1972	12,258,278	21,198	3.2	62	0.67	2
1973	1,240,970	4,188	5.3	0	10.78	4
1974	14,495,217	12,462	5.8	1	0.71	2
1975	5,000,000	5,160	5.7	0	10.92	3

*% canned is not included in number of indices indicating unavailability.

and price increased. The catch per delivery day rose slightly at Monterey but remained below 4 tons/day, indicating that poor availability caused the reduced catches.

Landings increased in 1962 but were still below 3,000 tons, and southern California followed with a good catch. But the mean annual price at Monterey dropped, whereas the catch per delivery day was better than 5 tons/day. This year the catch was probably suppressed because of lack of demand caused by loss of overseas markets during 1960 and 1961.

In 1966, an unusual set of circumstances took place. The catch was good, but all other indices show it was a poor year. Prices were high, but the catch per delivery day was low and the demand was not met, which resulted in good catches in southern California. Even though squid catches were good at Monterey, the demand for squid could not be met, indicating limited availability of squid.

In 1970, the same situation developed. The landings were relatively good, but the other indices indicated a poor season. The southern California catch reached record amounts in 1970.

In 1973, the Monterey squid fishery experienced its worst season in history. Annual prices paid to fishermen were high, but the catch per delivery day dropped very low, and southern California catches remained good.

Availability of squid at Monterey in 1973 was extremely poor.

The Monterey squid fishery rebounded in 1974 and experienced an excellent year with good catches and high prices. The price paid to fishermen remained high due to the high demand for frozen squid caused by low inventories from the 1973 season. The Monterey catches dropped in 1975 at a time when prices paid to fishermen were very high. Southern California had another record year, and clearly poor availability prevailed at Monterey.

The search for the cause of fluctuations in squid availability can now be approached with some knowledge of when squid yields have been poor. Red crabs, *Pleuroncodes planipes,* washed up on Monterey Peninsula beaches in the winter of 1969-1970 and 1972-1973. They had also been reported to have washed up on Monterey Peninsula beaches in the winter of 1959-60 (Glynn 1961). Many oceanographers explained the occurrence of these red crabs as a consequence of a strong Davidson current. Mean sea-level height is the best available measure of the strength of coastal currents (Reid and Mantyla 1976), and Avila is the closest station to Monterey at which data have been gathered over a sufficient time span. Regression of the catch per delivery day from 1960-1974 against the previous Avila fourth-quarter sea levels yielded a correlation coefficient of -0.63, meaning that 40% of the variability in catch per delivery day is associated with variations in sea level. There were few years in which fall sea-level heights were not inversely related to the success of the following summer fishery (Figure 8). High sea-level heights in the fall of 1958 were followed by a successful season in 1959, and the unsuccessful seasons of 1975 and 1976 were not preceded by high sea levels in the falls of 1974 and 1975.

CONCLUSION

The poor availability of squid at Monterey during 1952, 1958, 1960-61, 1966, 1970, and 1973 and 1975 was the primary reason for poor catches those years. Catches were also low in 1950, 1953, and 1962, but this was apparently due to lack of demand caused by a glut of canned squid from the peak World War II seasons and to a loss of overseas markets due to the poor years of 1960 and 1961.

High fourth-quarter sea levels and a strong Davidson current appear to be one set of factors often associated with poor availability of squid to the Monterey fishery the following summer.

ACKNOWLEDGMENTS

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DETECTION OF MARKET SQUID, *LOLIGO OPALESCENS*, WITH ECHO SOUNDERS

DOUGLAS L. VAUGHAN AND CONRAD W. RECKSIEK
Moss Landing Marine Laboratories
P.O. Box 223, Moss Landing, CA 95039

ABSTRACT

Schools of the squid, *Loligo opalescens,* were located with low (38-kHz) to high (200-kHz) frequency echo sounders in nearshore waters of the Southern California Bight and Monterey Bay during research cruises from May to August 1976. Verification of squid traces on echograms was accomplished by midwater trawling, jig fishing under lights, and visual observation. Two radically different behavior patterns are represented by the echograms: 1) continuous bottom-associated traces which can be resolved over a substantial frequency range (38-200 kHz); and 2) midwater plume-like traces which may be more effectively resolved at higher frequencies.

INTRODUCTION

Echo location of fishable squid concentrations is used in several fisheries. Examples of this include the Japanese fisheries (Flores 1972) of "surume-ika," *Todarodes pacificus*; "kaka-ika," *Sthenotensis bartrami;* "budo-ika," *Loligo budo;* "kensaki-ika," *Doryteuthis kensaki;* "yari-ika," *Doryteuthis bleakeri*; and the California market squid, *Loligo opalescens,* fishery of southern and central California.

Studies of squid aggregations using echo sounders have been carried out in Japanese waters. Shibata and Flores (1972) described echogram traces produced by 50- and 200-kHz echo sounders of various squid species during commercial fishing operations. Echo sounders have been used in describing *Todarodes pacificus* school size, diel behavioral changes, and depth distribution (Kawaguchi and Nazumi 1972; Suzuki et al. 1974).

This paper describes research on the acoustic detection of market squid, *Loligo opalescens*, conducted between May and August 1976. This work consisted of identifying the types of traces that squid produced on echograms from different types of echo sounders. Based on these traces, some aspects about market squid behavior are described.

METHODS AND MATERIALS

Echograms were collected from three separate echo sounders, which varied in frequency from 38 to 200 kHz, throughout the period of May to August 1976. These machines had differences in frequency, pulse length, pulse repetition rate, paper speed, type of paper, beam angle, and time-varied gain adjustments (Table 1).

They were primarily used at various locations between Santa Rosa Island and Santa Cruz, California

(Figure 1). The manual gain and white-line settings for each instrument at each location were adjusted for optimal reading of the echograms. Verification that the traces observed were those of *Loligo opalescens* was accomplished through visual observation, midwater trawling, and jig fishing under lights. The traces known to have been caused by this squid species are reproduced herein (Figures 2-6).

RESULTS

A Simrad EK-38 (38 kHz) and a Gemtronics GT-105 (200 kHz) were used simultaneously aboard the California Department of Fish and Game R/V *Alaska* from 28 May 1976 to 20 June 1976 (Cruise 76A4). Echograms that could be attributed to *Loligo opalescens* are

Figure 2 portrays echograms taken with the Gemtronics GT-105 and Simrad EK-38 at a night-light station on 8 June 1976 while at anchor in 29-m depth. The light was switched on at 0055. The ship was positioned at 33° 54.5' N and 120° 0.1' W, which is 2.7 miles southwest of East Point on Santa Rosa Island, California (Location 1, Figure 1). In the two hours spent at this station (0055-0255), 350 market squid were jigged; many squid were observed at the surface, along with occasional sightings of sharks, pelagic polychætes, and salps. Because of the high catch and numerous sightings of squid and the fact that only a few other marine organisms were observed, the traces at this station were assumed to be squid.

The Gemtronics echogram for this station showed dark, closely spaced, feather plume-like traces next to the surface after the night light was turned on (Figure 2-A). These traces remained for approximately 11 minutes, and their occurrence corresponded to visual sightings of squid near the surface. Two additional similar groups of plume-like traces occurred near the surface at various intervals throughout this station. The second group of traces appeared toward the middle of the station and lasted approximately 14 minutes; the third group occurred toward the end of the station and lasted approximately 4 minutes. The vertical extent of these traces over the entire station ranged between 2.3 and 11.3 m. Toward the end of the station, plume traces were also recorded near the bottom (Figure 2-B).

Throughout most of the station, the Simrad EK-38 recorded traces on and near the bottom which ranged in vertical extent from approximately 2 to 14 m. Figure 2-C is an echogram of the largest of these traces recorded.
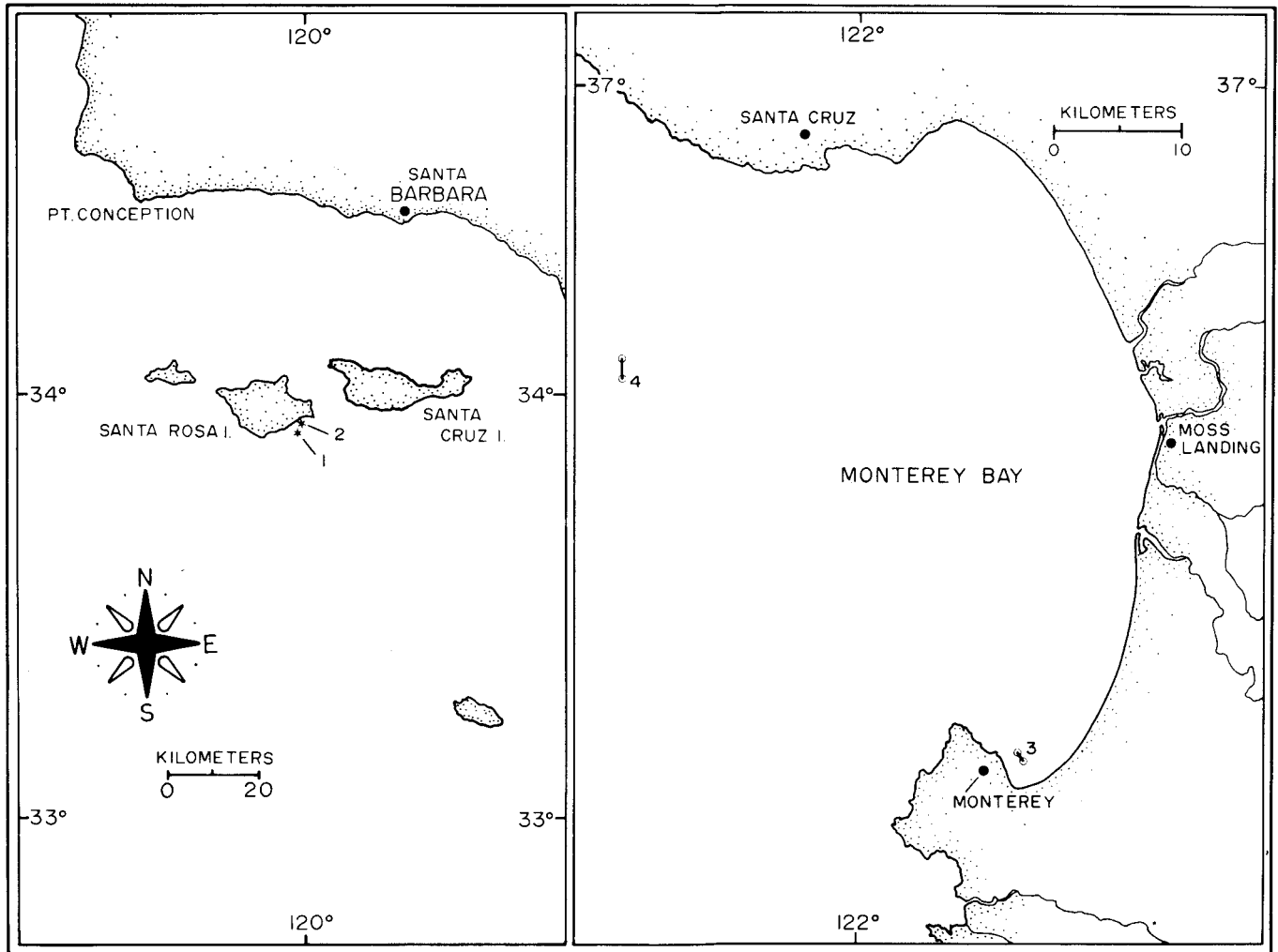
Figure 1. Midwater trawls (3, 4) and night-light stations (1, 2) where echo sounders were used in the detection of market squid May through August 1976.

Unlike the Gemtronic echo sounder, no large traces were recorded near the surface.

Figure 3-A and B are traces taken simultaneously with the Gemtronics and the Simrad EK-38, respectively, when the R/V *Alaska* was searching for squid at an estimated speed of 2 knots next to Santa Rosa Island. The mark with the letter "A" adjacent to it was made at the same time for both units. The primary trace represented a concentration of animals which was approximately 0.5 km long and extended from 2.3 to 14.5 m off the bottom. The ship's position at the time of the trace was approximately 33° 55.7' N and 120° 0.5' W (Location 2, Figure 1). After passing over the school once, the vessel doubled back over it, anchored, and the night light was switched on. Squid were caught soon after jigs were lowered to the bottom. This station began at 0340 on 8 June 1976 over a depth of 27.4 m. Figures 4-A and B show respective traces for the Gemtronics and Simrad

EK-38 taken at the beginning of the night-light station.

After the light was on for approximately five minutes, plume-like traces on the Gemtronics were appearing to rise toward the surface (Figure 4-A). By 0410, this sounder was recording a continuous bottom trace, which was about 3.7 m in height, and numerous "speckled" traces (Figure 4-C). These speckled traces were recorded as almost saturating the water column. At this time, adult squid were being jigged at a relatively fast rate; 500 were caught during the station. They were also visible in heavy concentrations at the surface and many were seen copulating. Other marine organisms visible were spiny dogfish, unidentified sharks, and pelagic polychaetes.

The EK-38 recorded dark bottom traces at times during the station and very faint traces in the water column above the bottom (Figure 4-B). Traces off the bottom were resolved to a much lesser degree than Gemtronics traces taken at the same time. Scattering was recorded

41

Figure 2. Echograms of market squid traces taken from the R/V *Alaska* 8 June 1976 at a night-light station near Santa Rosa Island (33° 54.5' N, 120° 0.1' W, depth 29 m), taken with A. 200-kHz Gemtronics GT-105, showing plume-like traces near the surface, recorded at the beginning of the station (approximately between 0055 and 0106 hours); B. 200-kHz Gemtronics GT-105, showing plume-like traces near the bottom, recorded midway through the station (approximately between 0150 to 0200 hours); C. 38-kHz Simrad EK-38, showing bottom traces assumed to be market squid.
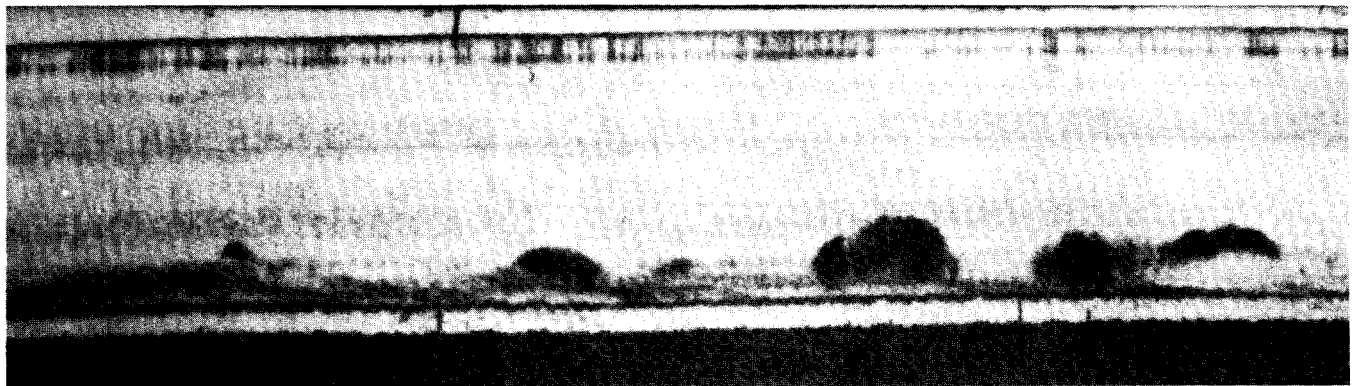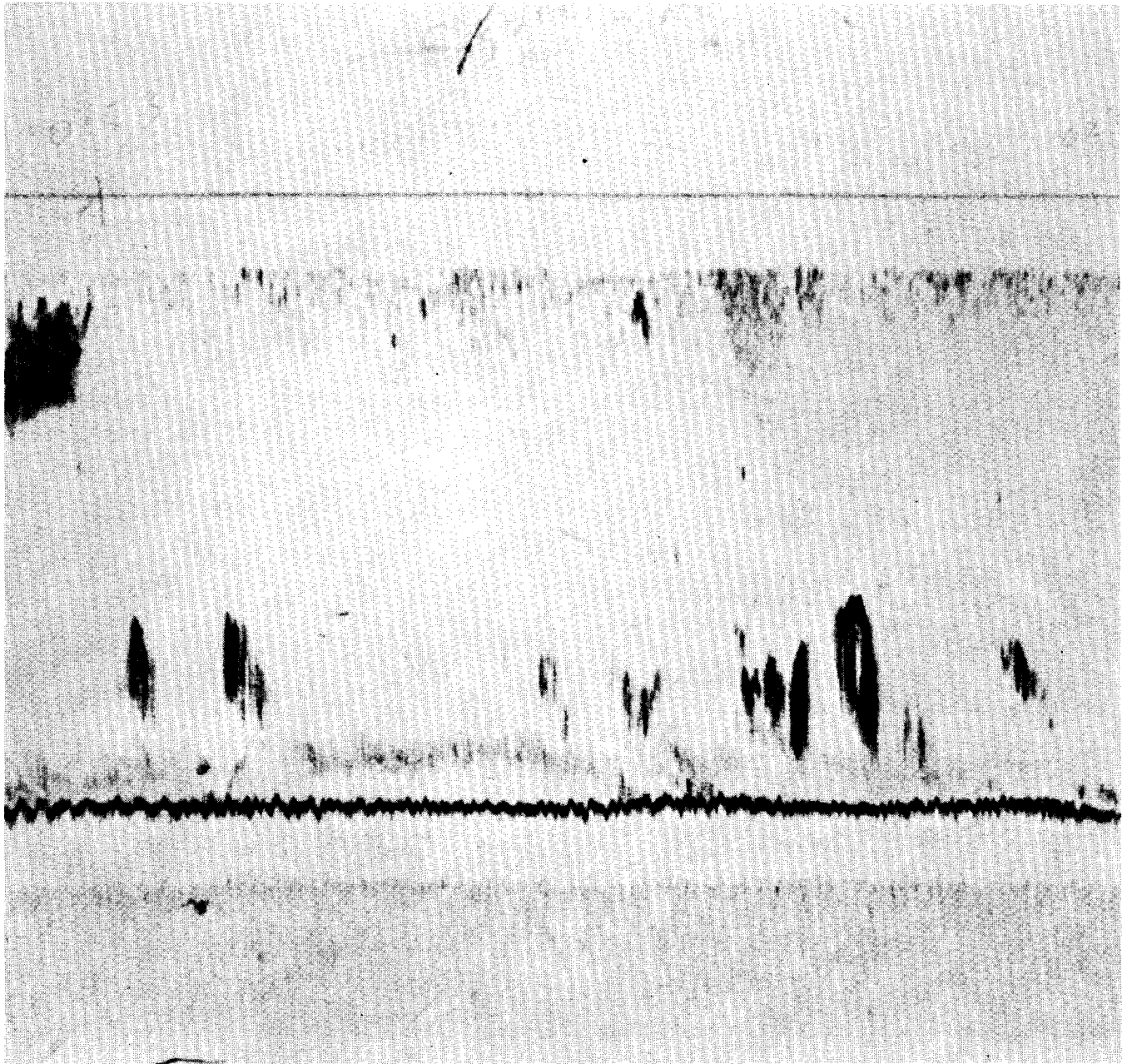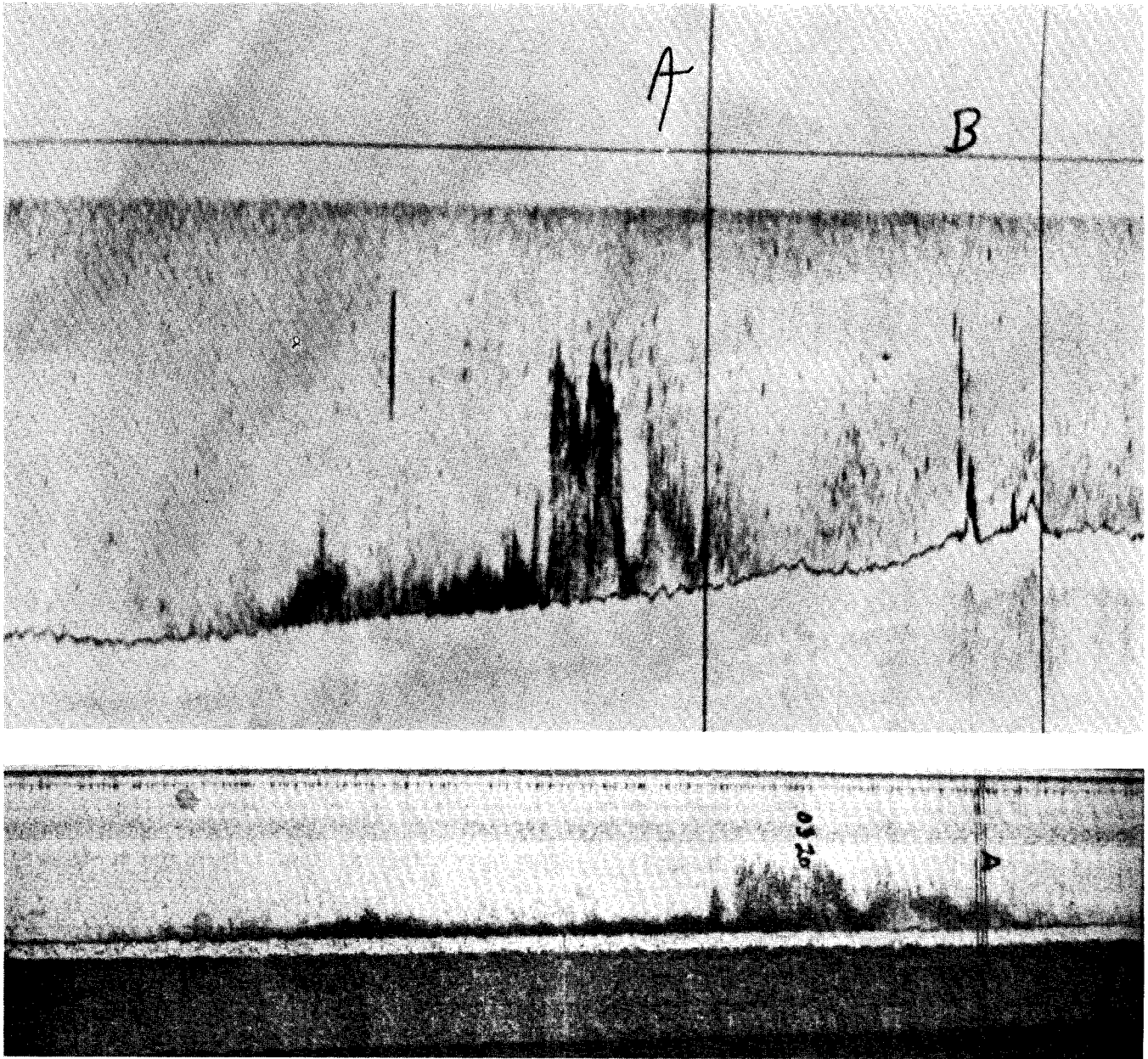
Figure 3. Echograms of market squid taken from the R/V *Alaska* traveling at an approximate speed of 4 knots while searching for squid next to Santa Rosa Island 8 June 1976. At Mark A on both echograms, the ship's approximate position was 33° 55.7' N, 120° 0.5' W; time was 0320 hours; A. taken with the 200-kHz Gemtronics GT-105 echo sounder; B. taken with the 38-kHz Simrad EK-38 echo sounder.
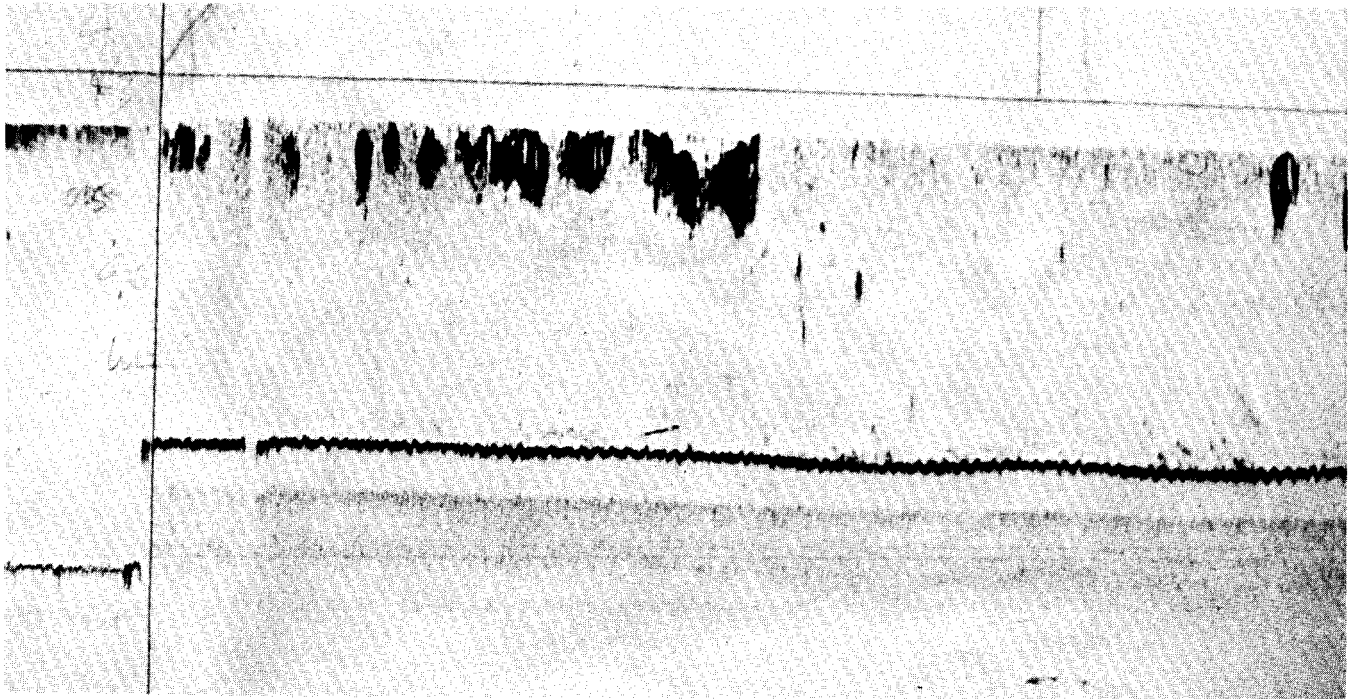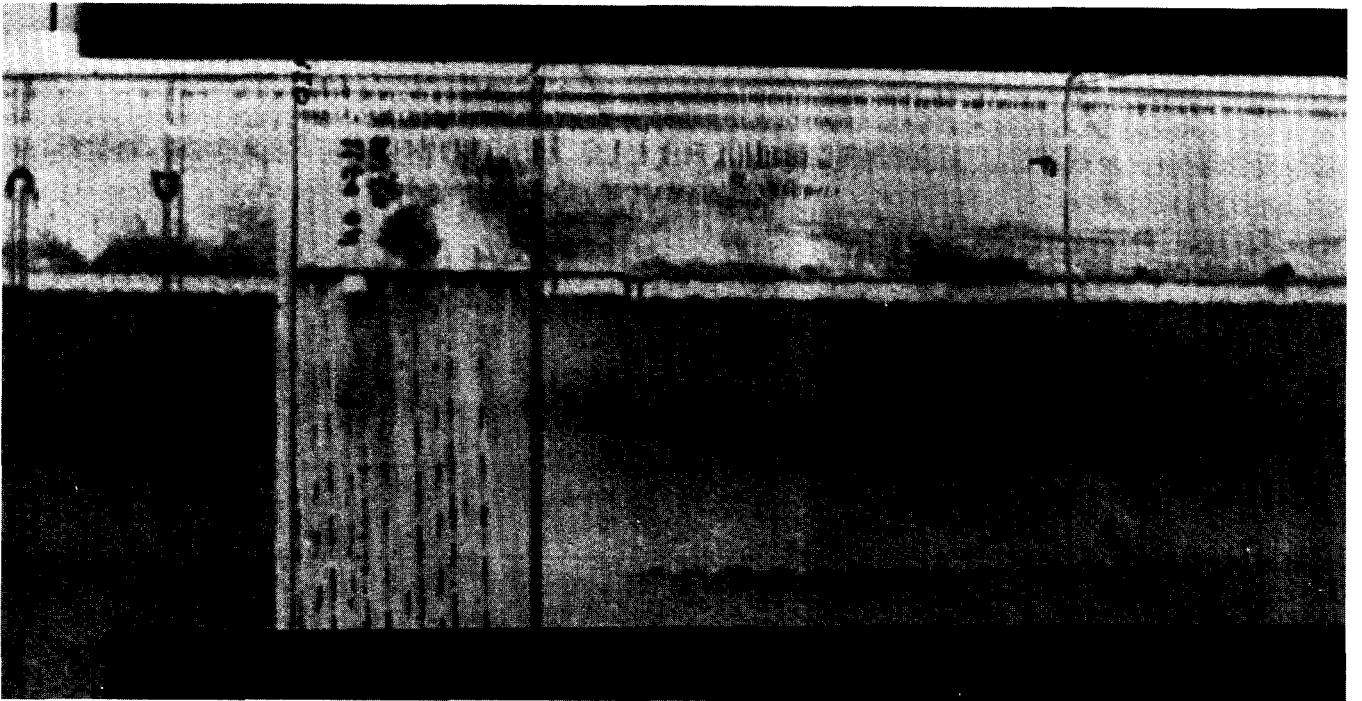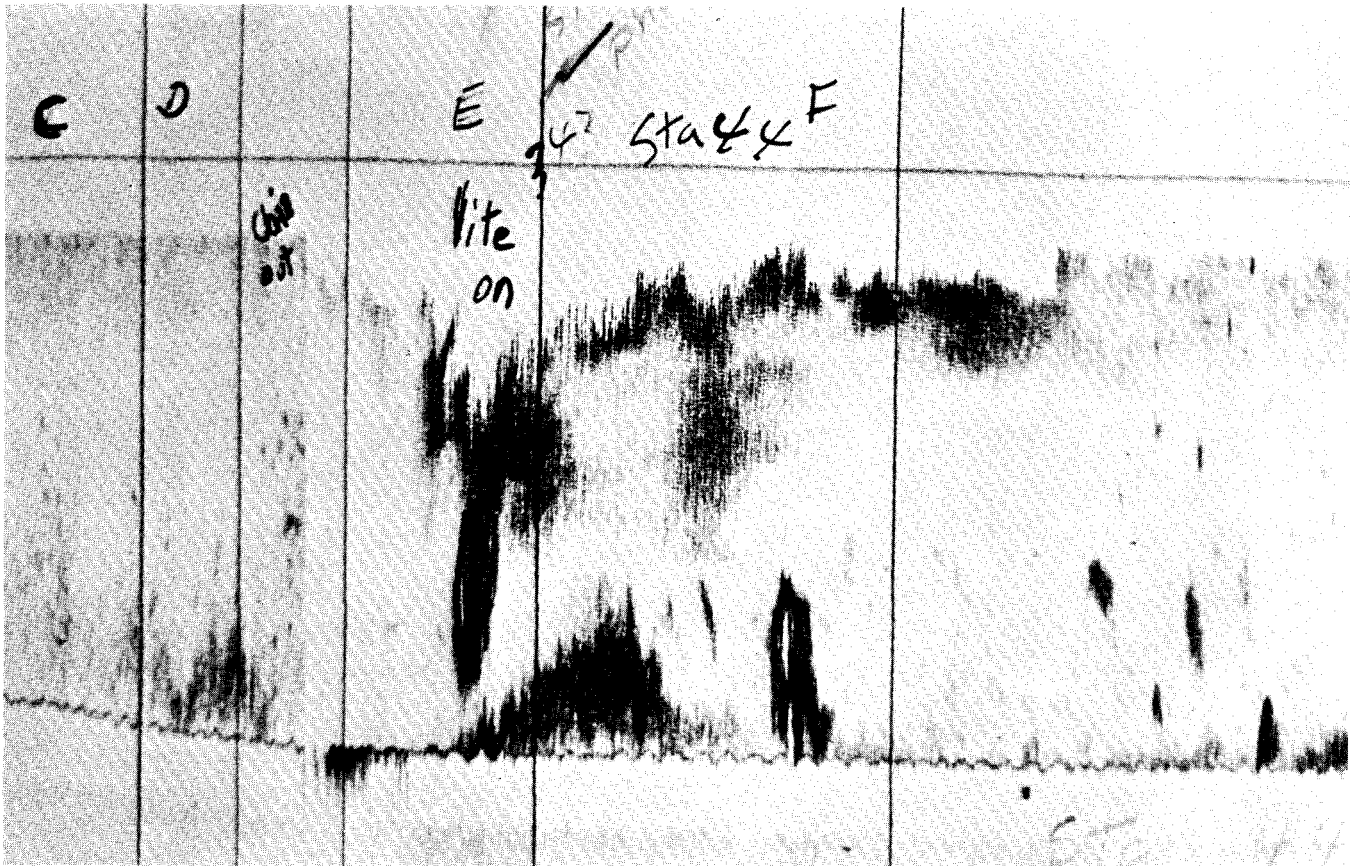
Figure 4. Echograms of market squid taken from the R/V *Alaska* 8 June 1976 at a night-light station near Santa Rosa Island (33° 55.7' N, 120° 0.5' W, depth 27.4 m): A. 200-kHz Gemtronics GT-105, taken at the beginning of the station, showing continuous squid traces along the bottom and plume-like squid traces rising toward the surface. The light was turned on at approximately 0340 hours (Mark E); Mark F was made at approximately 0344. The large dark trace that extends throughout the water column under the words "lite on" was caused by anchoring. B. 38-kHz Simrad EK-38, taken at the beginning of the station. Marks E and F were made at the same time as those shown on the Gemtronics in A. The continuous traces next to the bottom between these two marks were assumed to be market squid. Most of the scattering recorded above the bottom next to Mark E was caused by anchoring. C. 200-kHz Gemtronics GT-105, taken approximately between 0405 and 0433 hours, showing "speckle" traces almost saturating the water column and a continuous trace lying along the bottom. D. 200-kHz Gemtronics GT-105, taken between 0449 and 0510 hours, showing less traces as dawn approached.
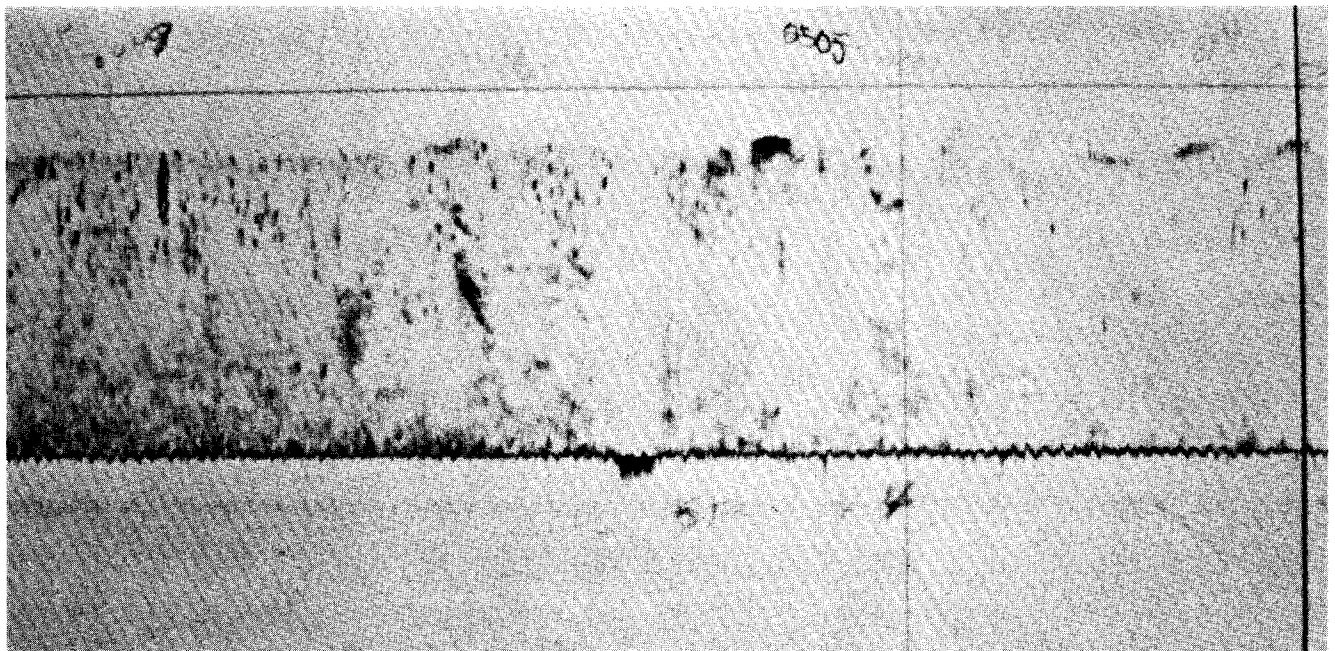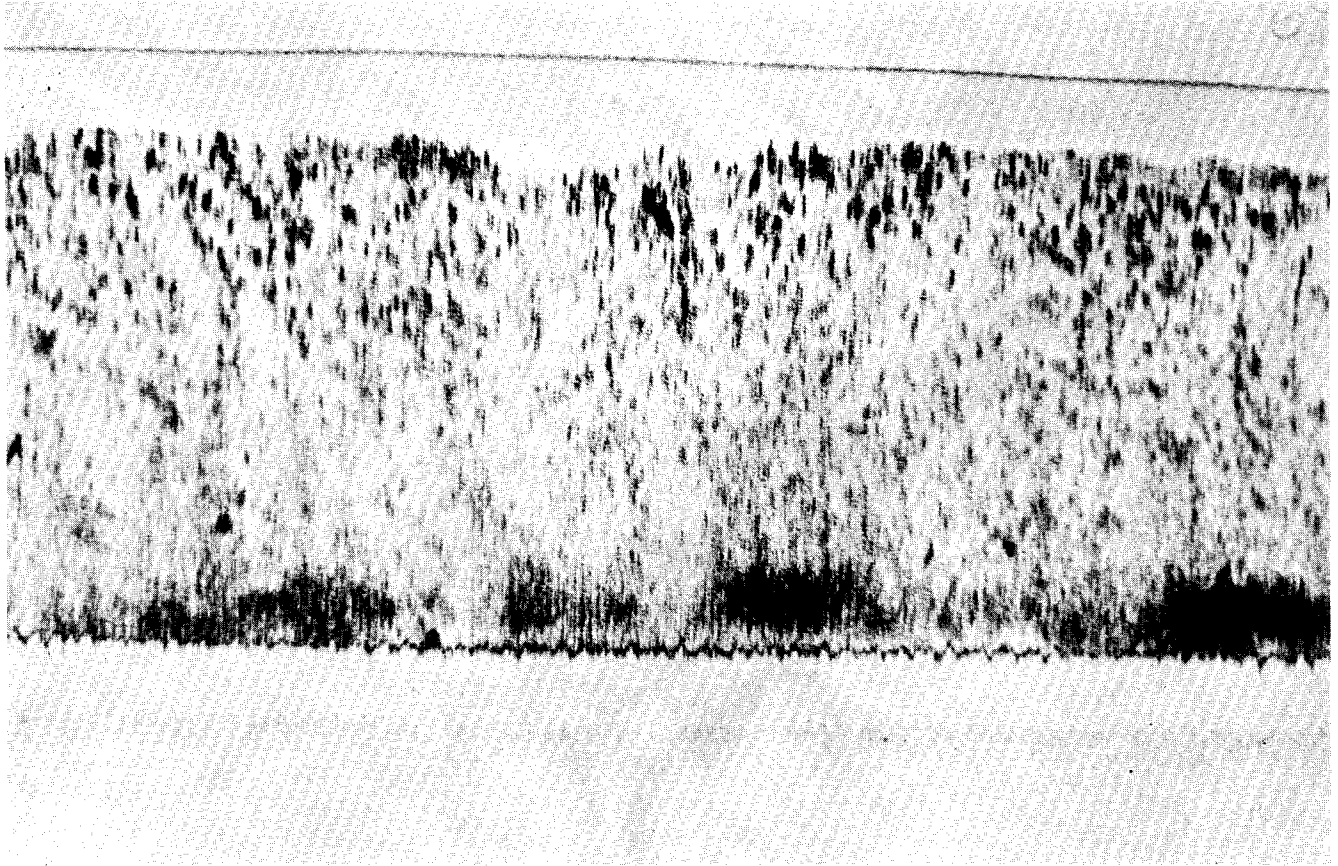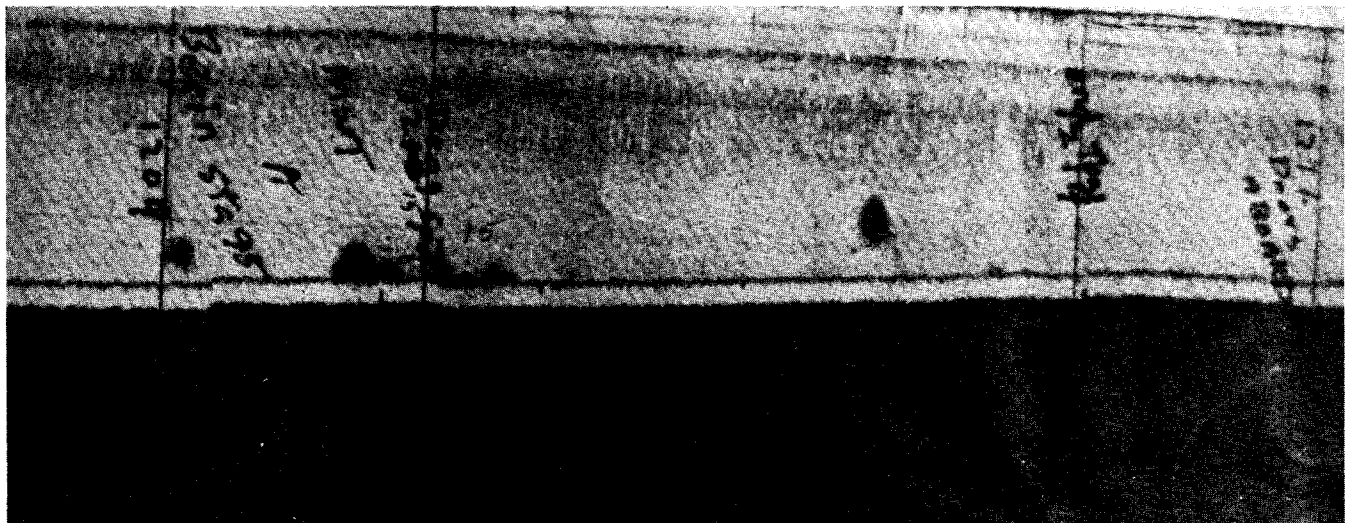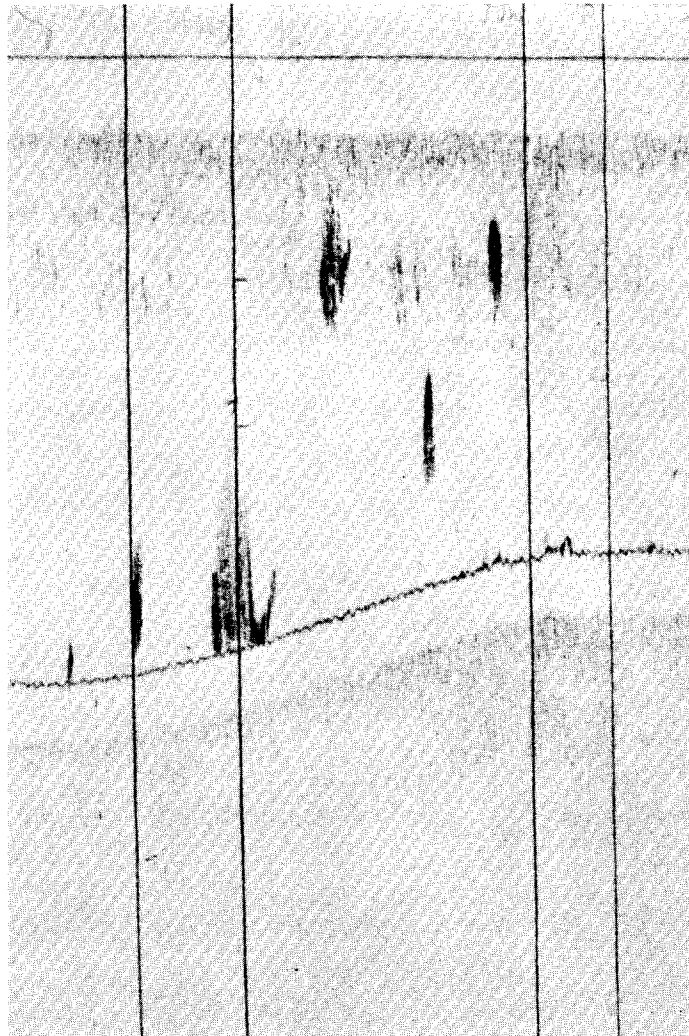
Figure 5. Echograms taken in Monterey Bay during a midwater-trawl station from R/V *Alaska* traveling at an approximate speed of 3 knots 20 June 1976 between 1215 and 1219 hours (36° 37.3' N, 121° 53.5' W to 36° 37.1'N, 121° 53.4' W). Marks correspond to stages in fishing the net: first mark shooting (1209); second mark to third mark trawl speed; fourth mark hauled (1226). A. 200-kHz Gemtronics GT-105. The three large plume-like traces are assumed to represent market squid. B. 38-kHz EK-38. The large plume trace within the trawl speed marks is assumed to represent squid and was recorded at the same time as the middle plume trace on the Gemtronics sounder in A.

throughout the water column; however, the scattering off the bottom did not look much different from the normal background that accompanies traces of most of the Simrad EK-38 echograms collected even when there were no squid. The light was turned on at approximately 0340; mark "E" on the echogram corresponds to this time. Mark "F" was made at approximately 0344. The continuous traces next to the bottom between these two marks were assumed to represent market squid.

As dawn approached this station and it became progressively lighter, less traces were recorded until almost none were on the echogram (Figure 4-D); less squid were caught with the fishing gear and less were observed on or next to the surface. At dawn, squid were no longer detected under the vessel.

Daytime traces of market squid were collected with the Gemtronics and Simrad EK-38 echo sounders (Figures 5-A and B, respectively) in Monterey Bay on 20 June 1976. These traces were recorded while the *Alaska* was towing a midwater trawl moving at a speed of approximately 3 knots (36° 37.3' N, 121° 53.5' W; 36° 37.1'N, 121° 53.4' W; Location 3, Figure 1). The trawl's head rope was at an estimated depth of 11 m, and its ground rope was estimated at 29 m. The catch was 1,646 market squid, 1 *Torpedo californica*, 1 *Pelagia*, 1 *Chrysaora*, 3 unidentified jellyfish, and 1 unidentified crab. The market squid had a mean dorsal mantle length of 117.6 mm with a standard deviation of 12.59 mm. The Gemtronics echogram for the trawl showed three large, dark, plume-like traces (Figure 5-A). The first one to appear made a trace that began at 7 m and continued to 14.1 m. The middle trace ranged from 16.4 to 23.5 m,

Figure 6. Echograms taken from the National Marine Fishery Service chartered R/V *Pacific Raider* while midwater trawling in Monterey Bay on the morning of 24 August 1976 (36° 50.5' N, 122° 9.5' W to 36° 49.8' N, 122° 9.5'W). Upper, taken from a Furuno net sounder (Model No. FNR-400). The head rope was recorded as the double black line toward the vertical middle of the echogram. The bottom line of the trawl was recorded as the black line underneath the head rope trace, and the ocean bottom can be seen as the rising black trace at the lower right hand side. The black trace toward the middle of the picture, which is between the head rope trace and the bottom line trace, is assumed to be squid. Lower, taken with a 50-kHz Japanese Radio Company zoom echo sounder (Model No. NJA-310). The area within the square to the right shows where the net was fishing in the water column at the time a large trace was recorded entering the net by the net sounder. The trace within this area is assumed to be squid.

TABLE 1

Specifications for Echo Sounders*
Used in the Detection of Loligo opalescens.

Echo Sounder	Research Vessel	Frequency (kHz)	Pulse Length (msec)	Pulse Repetition Rate (/min)	Beam Angle @ -3 db Loss	Paper Speed (mm/min)	Type Paper	Time-Varied Gain	Mount-ing
Gemtronics GT-105	Alaska	200	0.85	180	**	8	dry	no	side
Simrad EK-38	Alaska	38	3.0-0.3	96	20° along-ship; 13° athwart-ship	25	wet	yes	hull
Japan Radio Co. NJA-310	Pacific Raider	50	1-3	**	22°	~10	wet	no	hull

*These machines may possess mutiple specifications for the parameters listed. The specifications in this table hold for the echograms discussed in this paper.

**unavailable

and the last trace ranged from 8.4 to 14.1 m. Because of the high catch of squid and low numbers of other species found in the net, these traces were assumed to represent squid. The Simrad EK-38 recorded one major plume between 14.9 and 27.4 m (Figure 5-B). The target making this trace was assumed to be the same as the target causing the middle trace on the Gemtronics. Both occurred at a similar depth range and both took place 2 minutes, 48 seconds after the onset of the trawl.

Figure 6 shows echograms taken from a 50-kHz Japan Radio Company zoom echo sounder (Model No. NJA 310) during a midwater trawl operation and an echogram from a Furuno net sounder (Model No. FNR 400), which was operating simultaneously. The unit of the net sounder that was placed on the head rope of the midwater trawl consisted of an upward- and downward-facing transducer that operated at 75 kHz and a transmission transducer that operated at 50 kHz. Consequently, targets which passed into the net were detected at 75 kHz and received by the recording unit at 50 kHz. Both sounders were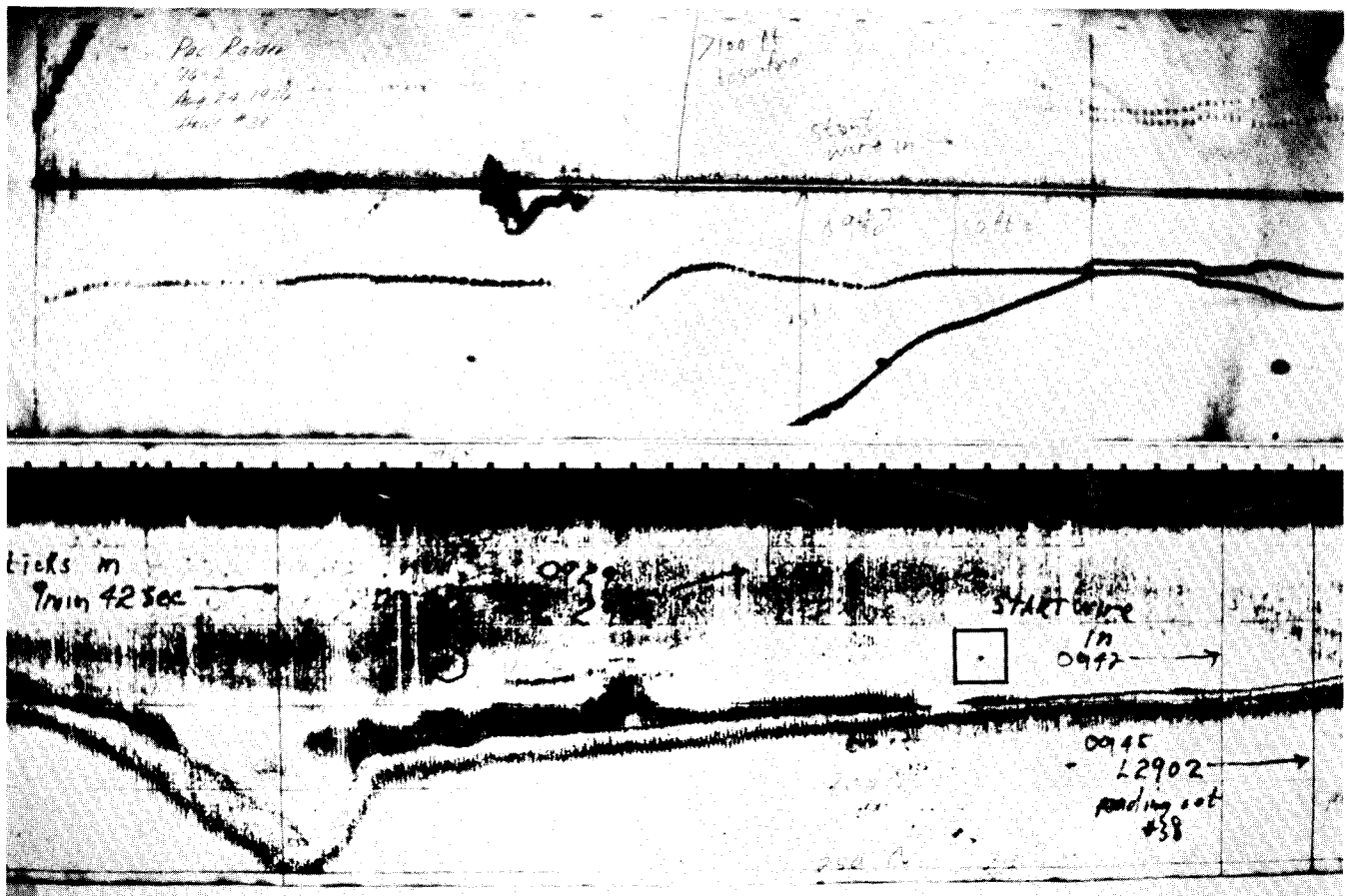 used aboard the National Marine Fishery Service chartered R/V Pacific Raider while midwater trawling in Monterey Bay on 24 August 1976 between 0934 and 0942 (36° 50.5' N, 122° 9.5' W; 36° 49.8' N, 122° 9.5' W). During the tow, the net sounder recorded a large, dark trace entering the net (Figure 6, top). At the time this trace was recorded, the net was assumed to be fishing at 125 fathoms. A square surrounds the trace of the JRC echo sounder echogram of what was presumed to be the catch entering the net (Figure 6, bottom). The entire catch consisted ot more than 200 squid, averaging a dorsal mantle length of 83.7 mm with a standard deviation of 7.98 mm, and four medusae. A continuous trace along the bottom, which extended between 20 and 60 m above the bottom, was recorded by the echo sounder as well.

DISCUSSION AND CONCLUSIONS

Schools of market squid were shown to produce three distinct type of traces on echograms. The first was a feather plume-like trace that appeared when schools were pelagic (Figure 2-A, 2-B, 4-A, 5-A, 5-B). The second type was a more-or-less continuous bottom trace that appeared when schools were on or near the bottom (Figures 2-C, 3-A, 3-B, 4-A, 4-B, 4-C). The continuous trace recorded along the bottom in the lower portion of Figure 6 may be squid as well. In the latter case, the net was fishing close to the shoal represented by this trace when two hundred squid were captured. The third type of trace consisted of "speckles" scattered throughout the water column when squid were attracted toward the surface at a night-light station when the ship was anchored (Figure 4-C). At the time these latter traces were recorded, squid were viewed from the surface to be in large numbers, some of them copulating. Therefore, each of these speckles probably represented individual squid, a copulating pair, or a small aggregation. Squid aggregated too close together to be resolved as individuals in the continuous and plume traces. The entire surface area on the echogram of most of these traces known to be squid was darkened.

Plume-like traces on echograms are caused by schools being less than the diameter of a cross-section of the acoustic beam and by the schools being more or less elipsoidal in shape (Cushing 1973). A continuous trace is made when targets remain under an echo sounder beam for a relatively long period of time. This trace can be caused by the ship being stationary over a stationary target or a ship moving on top of a large school or scattering layer (Cushing 1973). Usually, the horizontal distance of the school is much larger than the cross-sectional diameter of the acoustic beam at that depth. Consequently, this study has found squid to aggregate either in large numbers close to the bottom or in smaller numbers in pelagic schools.

The traces that market squid have been shown to make in this study resemble those that other researchers have found. Shibata and Flores (1972) using 200-kHz and 50-kHz echo sounders have shown plume-like traces for various species of squid caught in Japanese waters off a moving boat and when squid were rising to the light at a night-light station. Kawaguchi and Nazumi (1972) have shown similar plume-like traces taken in the day for Todarodes pacificus with 200- and 75-kHz echo sounders. Mais (1974), using the 38-kHz sounder described in this paper, has shown Loligo opalescens to make a more-or-less continuous layer which appears next to the bottom.

Market squid were detected with 38-kHz, 50-kHz and 200-kHz echo sounders. The 38-kHz Simrad EK-38 and the 200-kHz Gemtronics GT-105 recorded squid traces both in the day (Figure 5) and night (Figures 2 through

4). The "speckle" traces that appeared on the Gemtronics echogram during a night-light station (Figure 4-C) were not apparent on the Simrad EK-38 echogram when these units were operating simultaneously. More plume traces of market squid appeared on echograms of the Gemtronics than the Simrad EK-38 when both were operating simultaneously. At the first night-light station discussed (Location 1, Figure 1), the Gemtronics recorded many plume traces (as the ones shown in Figure 2-A); the EK-38 recorded none. The Gemtronics recorded three plume traces during the midwater trawl in Monterey Bay (Figure 5-A) while the EK-38 recorded only one trace (Figure 5-B).

In this study, it is difficult to determine whether the Gemtronics has superior specifications, such as higher frequency, to the EK-38 for locating small pelagic groups of squid, or whether the difference in the amount of traces on echograms was due to the different locations of the transducers. The transducer of the Simrad EK-38 was located on the hull, whereas the transducer of the Gemtronics was located on th hull, whereas the transducer of the Gemtronics was located amidships on the port side during midwater trawling operations and amidships on the starboard side under the light during night-light stations. It is likely that the Gemtronics picked up more squid plumes because squid schools were more likely to be insonified at light stations by a transducer which is next to an attracting light, squid schools were closer to the Gemtronics' transmission axis during the midwater trawl, and small squid aggregations were better detected with the higher frequency echo sounders. Suzuki et al. (1974) found that a 200-kHz echo sounder recorded squid more clearly than a 75kHz sounder; and Kawaguchi and Nazumi (1972) concluded that the optimum specifications of an echo sounder for squid detection were a frequency between 75 kHz and 200 kHz, narrow beams, and a minimum pulse length.

• Echograms at night-light stations demonstrated the fact that lights attract market squid during the night (Figures 4A and C). At dawn, the light lost its effectiveness to attract squid, as demonstrated by the lack of targets recorded in Figure 4-D. Therefore, either the squid scattered, moved as a school to a different location, or moved so close to the bottom that they became undetected by the sounders. Light attraction is a common phenomenon for several commercial squid species. Kawaguchi and Nazumi (1972) have demonstrated with echo sounders that *Todarodes pacificus* is lured to lights at night; and Shibata and Flores (1972) showed the same thing to occur with other species of squid caught in Japanese waters.

The description of traces on echograms caused by market squid was needed before echo sounders could be considered a useful tool in deriving information about this species. Therefore, this work is considered to be ar

essential precursor to acoustic management and behavioral studies conducted on market squid. The results in this study indicate that at least two behavioral modes can be resolved with echo sounding equipment from a moving ship. Extensive, continuous bottom-associated traces, which Mais (1974) and we have observed, probably represent concentrations that may develop only at certain times of the day, seasons, prey densities, maturity, etc. We are reasonably certain that they may occur in shallow (20-m) or deep (< 150-m) water. Once located, concentrations or shoals or this sort offer some prospect of being surveyed with a view toward determining biomass. The pelagic behavioral representations we have observed, i.e. plume traces, appear to represent small, perhaps feeding, groups of swiftly-moving animals. These squid schools are apparently quite difficult to sample and identify acoustically and offer less hope of usefulness for biomass estimating.

ACKNOWLEDGMENTS

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PREY COMPOSITION OF THE MARKET SQUID, *LOLIGO OPALESCENS* BERRY, IN RELATION TO DEPTH AND LOCATION OF CAPTURE, SIZE OF SQUID, AND SEX OF SPAWNING SQUID.

KONSTANTIN A. KARPOV
The Resources Agency
California Department of Fish and Game
California State Fisheries Laboratory
350 Golden Shore, Long Beach, CA 90802

GREGOR M. CAILLIET
Moss Landing Marine Laboratories
P.O. Box 223
Moss Landing, CA 95039

ABSTRACT

Squid feeding was investigated for Monterey Bay and adjacent areas. Squid were found to feed mostly on crustacea and to a much lesser degree on fish, cephalopods, gastropods, and polychaetes. Animals from deeper offshore waters fed more on euphausiids and copepods. Inshore, off the spawning ground, euphausiid feeding still dominated, although to a lesser degree. Mysids, megalops larvae, cephalopods, and fish were more important in these waters. On the spawning ground, feeding habits changed a great deal. Here crustacean feeding still dominated, although euphausiids were lacking from the diet. Demersal feeding became most important, with such items are megalops larvae, egg-like spheres, juvenile gastropods, and nereid polychaetes comprising the diet. Little difference in prey composition was found between sexes on the spawning grounds. Male squid tended toward larger meals (in terms of number of megalops larvae), and there was a more frequent occurrence of cephalopod fragments. A comparison of large and small squid from non-spawning ground areas revealed little difference in prey composition. Larger animals (101- to 180-mm mantle length) fed slightly more on euphausiids, cephalopods, and fish than smaller squid (21- to 100-mm mantle length).

INTRODUCTION

This study involves an analysis of the prey composition of the common Pacific market squid, *Loligo opalescens* Berry. Recent works by Fields (1965) and Loukashkin (1977) have determined the gross composition of this squid's diet but failed to resolve specific problems such as how this diet is affected by the habitat and biological state of the animal. Fields (1965) examined 106 squid stomachs with contents, obtained from subsampling commercial fish seiners and squid lampara boats in the Monterey Bay area. Most of these samples were taken from night catches and only from nearshore areas. Loukashkin (1977) examined 331 *L. opalescens* with contents. These samples were collected throughout the California coast but again from predominantly night catches. Loukashkin (1977) made no attempt to distinguish the samples caught on the spawning grounds from those caught in other nearshore and offshore areas. The purpose of our study is to evaluate the effect of depth and location of capture, size of squid, and sex of spawners on the prey composition of *L. opalescens*.

MATERIALS AND METHODS

Prey were identified from samples of *Loligo opalescens* taken from a variety of sources. Sampling was limited to Monterey Bay and its adjacent areas from Point Sur to Pigeon Point, California (Figures 1-3).
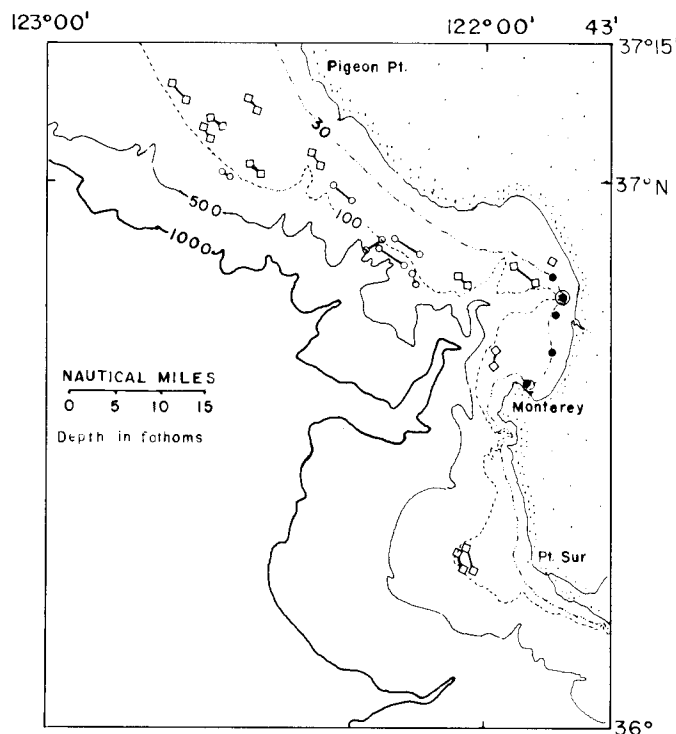
Figure 1. Locations of midwater and bottom trawls; Point Sur to Pigeon Point: ◊ = Bottom trawls day; ○ = Midwater trawls day; ● = Midwater trawls night.

These were obtained from directed bottom and midwater trawls aboard three research vessels: The California Department of Fish and Game R/V *Alaska*, the National Marine Fisheries Service R/V *Cobb*, and the R/V *Pacific Raider*, leased by the National Marine Fisheries Service. Samples were also taken from commercial squid, anchovy, and bottom-trawl catches.

The R/V *Alaska* used a large midwater trawl, as described by Ally and Mais (1975), with a ½-inch (1.27-cm) stretch mesh cod end netting, during June 1976. A total of seven samples taken in the Monterey Bay area were used in this study, with only two of these taken during daylight hours. All samples were taken at depths less than 40 fathoms (73.2 m; Figures 1 and 2). The R/V *Pacific Raider* used a large 60 by 60-foot (18.3 x 18.3-m) Herman Engel midwater trawl, with a 1½-inch (3.8-cm)

mesh cod end net. The R/V *Cobb* used an Eastern bottom trawl, having a 94-foot (28.7 m) lead rope, equipped with roller gear and a 71foot (21.6 m) lead rope. The cod end had a liner with 1¼-inch (3.2-cm) stretch mesh. A total of 14 samples were taken by both these vessels between Moss Landing Harbor and Pigeon Point, California, during August 1976. Samples were taken during daylight hours, at depths greater than 40 fathoms (73.2 m; Figures 1 and 2).

Squid taken on the spawning grounds in Monterey Bay included two samples from the R/V *Alaska* and subsamples of commercial squid catches. All samples were taken within a few miles of Monterey harbor at depths less than 20 fathoms (36.6 m; Figure 2). The commercial catches were subsampled while unloading between 24 September and 28 October 1975. During this period ten different samples were taken from seven different vessels. The squid were landed using lampara nets as described by Fields (1965). All catches were made between 2300 and 0800 hours.

The commercial anchovy fishery at Moss Landing, California, was also subsampled. *L. opalescens* can be taken directly from the conveyor belt while these boats are unloaded (Cailliet et al. 1976). Anchovies are fished in Monterey Bay using purse seine (Messersmith 1969), and these nets had a maximal depth penetration of 35 fathoms (64 m). Twenty samples were collected between 5 September 1975 and 10 March 1976. The hauls sampled were all taken during night hours with none of these taken near the spawning grounds (Figure 3).

Subsampling commercial bottom trawlers yielded three samples of squid from two separate vessels. These were taken on 24 September and 19 December 1975 and 9 January 1976. Depths of sampling were between 47 (86 m) and 80 (146 m) fathoms. Two of the samples were taken off Point Sur, and one was taken off Point Pinos, Monterey (Figure 1). Both vessels used large trawls with a 4½-inch (11.4-cm) stretch mesh cod-end net.

In addition, an incidental sample of *L. opalescens* was collected by the R/V *Tage* of Hopkins Marine Station, using a small otter trawl with a 24-foot (7.3-m) head rope and a ¼-inch (0.6-cm) stretch mesh cod-end liner. This sample was taken north of Moss Landing Harbor (Figure 2) at a depth between 10 and 20 fathoms (18.3 to 36.6 m) on 9 March 1976.

A maximum of ten squid with contents were analyzed in detail for prey compositioin from any one sample. These animals were first sexed, and their dorsal mantle lengths were recorded. Then, the stomachs were removed, and the contents were sorted, identified, and enumerated. Prey were identified to the lowest possible taxa. Rarely were whole organisms encountered in the stomachs examined, and for this reason key fragments had to play the major role in the identification process. Identification to the species level could not often be accomplished. Some
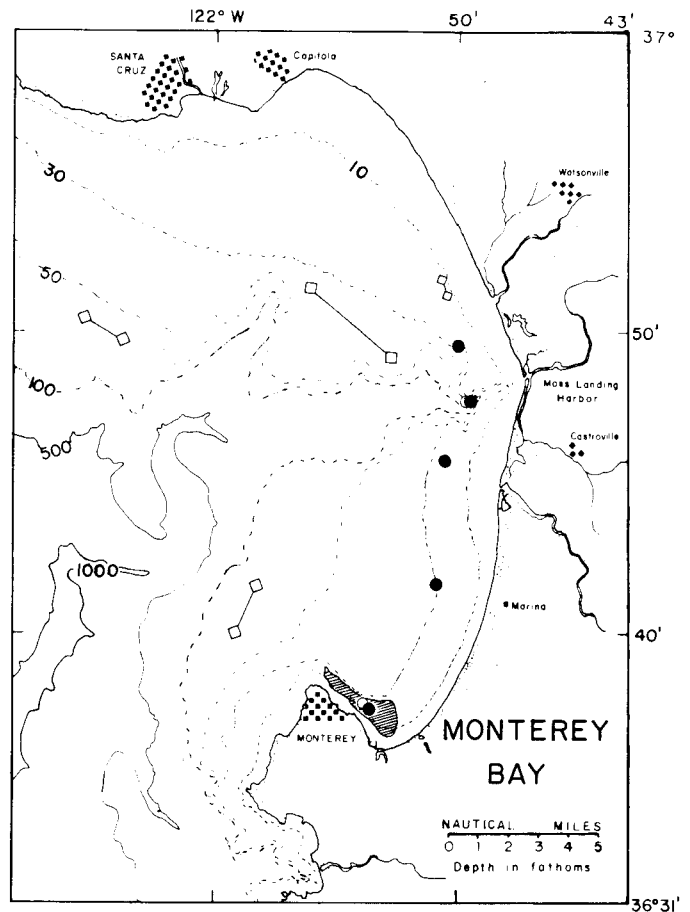
Figure 2. Locations of midwater and bottom trawls in Monterey Bay: ◊ = Bottom trawls day; ○ = Midwater trawls day; ● = Midwater trawls night; ■ = Squid spawning grounds.

species of crustacea were identified from a reference collection in the museum at Moss Landing Marine Laboratories. Squid could be individually recognized by using their beaks as a taxonomic tool. Recognition to the family level was possible using the key developed by Clark (1962), and some species could be identified by using the beak drawings furnished by Pinkas et al. (1971).

Most other identifications were more generalized. Crustaceans such as mysids, euphausiids, megalops larvae, amphipods, and shrimp possess distinctive eyes, mandibles, statoliths, and other parts that when taken together offer distinctive recognition. A collection of detailed drawings of such parts was assembled to aid prey recognition.

To assess the number of stomachs needed to adequately reflect feeding habits of the squid population, plots of cumulative numbers of taxa encountered per stomach were constructed for squid captured away from the spawning ground (Figure 4, upper) and from the spawning ground (Figure 4, lower) using 50 randomly selected squid stomachs for each category. Both plots leveled off at about 20 squid, indicating that this number
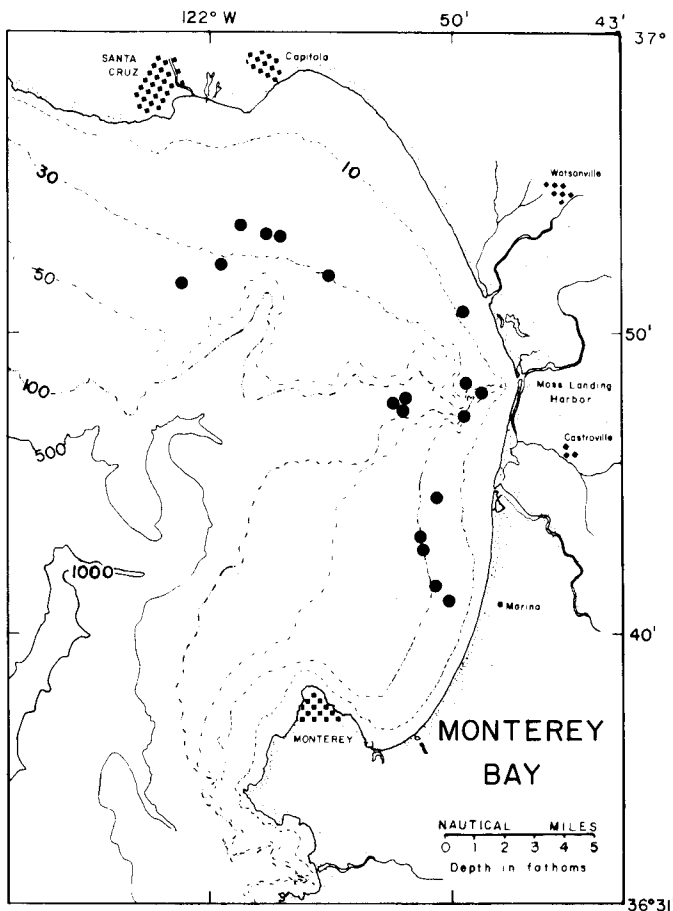
Figure 3. Locations of commercial anchovy seine sets in Monterey Bay.
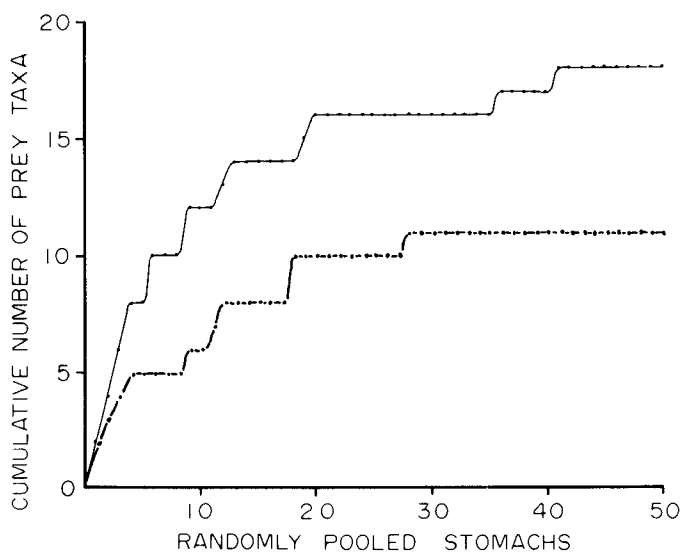
Figure 4. Cumulative sum of new taxa identified from the stomachs of 50 randomly selected *Loligo opalescens*. Upper curve is for non-spawning-ground samples, and lower curve is for spawning-ground samples.

of stomachs is sufficient to represent a valid comparison in any category. The smallest set of categories compared was between sexes on the spawning grounds, with 24 females and 27 males sampled.

The fragmented and often well-digested state of the stomach contents made counts of individual prey difficult and relative volume determinations impossible. Therefore, counts were based on pairs of eye lenses, mandibles, statoliths, otoliths, or polychaete jaws. Counts were not based on paired soft parts, such as decapod eyes, which were subject to digestion. Occasionally, stomachs were largely distended and filled with numerous euphausiid mandible pairs. These stomachs were divided into approximate halves; one portion was enumerated and the other portion was qualitatively examined. In such cases, counts were doubled.

A modified form of the Pinkas et al. (1971) "index of relative importance" was calculated in each comparison of depth, location, and size of squid for the major prey types eaten. The index was modified by using only numerical importance and frequency of occurrence. The numerical importance of a particular item was the percentage ratio of its abundance to the total abundance of all items in the contents. Its percent frequency of occurrence was the percentage of squid examined that contained at least one individual. The product in percents [(number) x (frequency)] is the index of relative importancet, which ranges from zero, when both values are zero, to 10,000 when both indices are 100% (a monodiet).

Percent frequency and number histograms were constructed for comparison of squid sizes, depths of capture, location on or off the spawning grounds, and the sexes of spawning-ground squid. Non-spawning squid were grouped into two size categories for comparison. Animals with 21- to 100-mm mantle lengths were compared to those with 101- to 180-mm mantle lengths. These two categories equally divided the number of animals yet retained a significant number of shallow-water and deep-water animals in each category.

Deep-water samples were defined as those taken from depths of at least 40 fathoms (73.2 m). These categories were somewhat arbitrary since the gear used did not sample at discrete depths. These trawls included most of the day midwater and bottom-trawled samples. Samples were considered shallow regardless of bottom depth when they were taken from water depths of less than 40 fathoms. These included all anchovy hauls, R/V *Alaska*, and R/V *Tage* samples. No samples taken near the spawning grounds were included in either category.

Rank correlation coefficients and indices of species similarity were calculated for these comparisons. The Spearman rank correlation test (Fritz 1974) was used to compare ranks of prey items, and the "percent similarity index" was used to examine the degrees of similarity

for comparisons of percent by number (Silver 1975). This index has no significance levels but serves to illustrate relative similarities between comparisons.

RESULTS

Prey Determination—Large versus Small Squid

In general, squid fed mostly on crustacea and to a much lesser degree on fish, cephalopods, gastropods, and polychaetes (Table 1). In most categories, euphausiids and copepods dominated the diet, but other crustaceans such as mysids, megalops larvae, cumaceans, and amphipods were important food items.

TABLE 1
Index of Relative Importance in Prey Composition

	Squid Size		Sample Location		
			Deep	Shallow	Spawning
	Small	Large	Water	Water	Grounds
Number of Squid	123	103	134	94	52
Crustacea unknown	73.3	17.5	23.8	135.2	95.4
Euphausiacea.............	3988.0	5400.0	6552.2	1553.4	0.0
Copepoda...............	97.5	37.5	103.8	1.0	0.0
Mysidacea	7.4	10.6	6.3	28.2	54.7
Megalops	4.9	0.0	0.1	23.3	1088.0
Natantia	0.2	0.6	0.0	1.9	0.0
Cumacea	12.2	0.0	2.6	1.0	0.0
Amphipoda	0.0	0.1	0.1	0.0	11.3
Ostracoda...............	0.0	0.1	0.1	0.0	0.0
Cephalopoda (whole)......	16.2	9.7	2.6	187.6	0.0
Gastropoda	5.0	1.2	1.9	5.7	295.8
Radiolaria...............	0.0	0.4	0.1	1.0	0.0
Polychaeta	0.0	0.0	0.0	0.0	24.9
Fish....................	2.0	8.8	1.3	44.8	11.3
Miscellaneous	–	–	–	–	197.2

A comparison of prey composition of large (101- to 180-mm mantle length) versus small (21- to 100-mm mantle length) *Loligo opalescens* from off the spawning grounds revealed few major differences (Figure 5, Table 1). Both size categories fed mostly on crustaceans, primarily the euphausiids, *Euphausia pacifica* and *Thysanoessa spinifera*. Other crustaceans taken included calanoid copepods; cumaceans; mysids; and the shrimp, *Sergestes* sp.

In both size categories, cephalopods and other non-crustaceans played a small role in the diet. Whole cephalopods eaten included *Gonatus* sp. and other *L. opalescens* individuals (cannibalism). Fragments of *L. opalescens* were also ingested and were most often identifiable as tentacle tips. Fish eaten were either unidentifiable species or *Engraulis mordax*. Gastropods and bottom debris were also ingested.

Histograms of percent frequency and percent by number of prey species indicated that large squid fed more frequently on euphausiids, cephalopods (whole and fragments), and fish (Figure 5). Rare taxa encountered only in the large squid feeding were the amphipod, *Jassa*
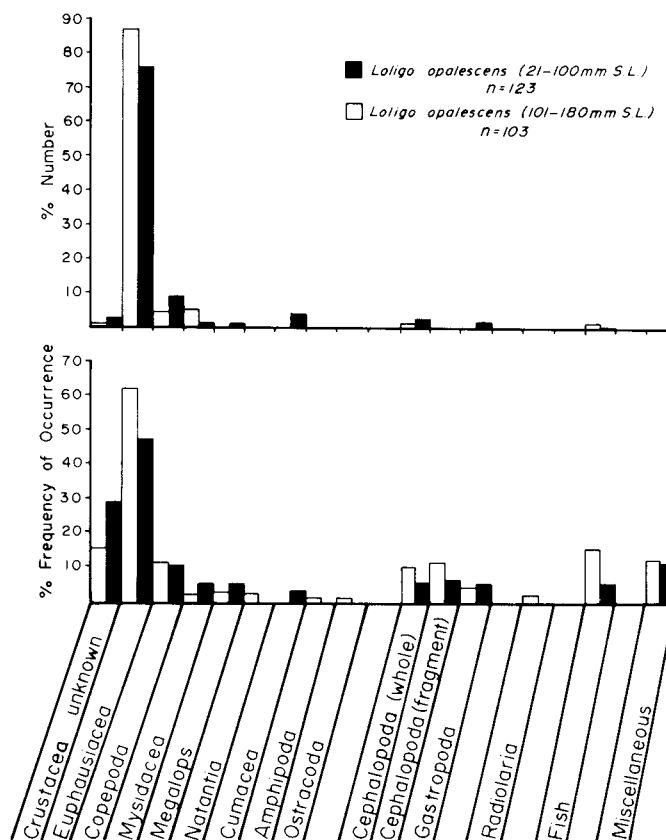
Figure 5. Comparison of prey frequency and number by size for non-spawning squid.

sp., ostracods, and radiolarians. Small squid fed more frequently on other crustaceans such as megalops larvae and cumaceans. Few inferences can be drawn from percent by number of prey species since both size classes were overwhelmed by the number of euphausiids eaten (Figure 5). The percent similarity index between the two size groups was high (84.9%), and the Spearman rank correlation test showed these two groups to have similar proportions of food items in percent frequency of occurrence ($P \leq 0.025$), but not in percent by number (Table 2).

Prey Determination—Deep versus Shallow Water

Comparison of prey composition by depth of capture revealed major differences (Figure 6, Table 1). Squid captured in deeper water fed more frequently on euphausiids and copepods. Squid taken nearer the surface fed far less frequently, although still predominantly, on euphausiids, whereas fish, whole cephalopods, mysids, and megalops larvae were more important to these squid. Despite a relatively high similarity index (71.8%), no significant correlation of prey item ranks was found in either percent frequency or occurrence or percent by number of prey species between deep and shallow water (Table 2).

TABLE 2

**Comparison between Sizes and Locations
Using Percent Similarity Index (P.S.I.)
and Spearman Rank Correlation Coefficient (r_s)**

	Percent Frequency of Occurrence	Percent by Number	
	r_s	P.S.I.	r_s
Large squid versus small squid (101-180 DML vs. 20-100 mm DML	0.699*	84.9	0.506 n.s.
Deep samples vs. shallow (0-40 fathoms = shallow)	0.549 n.s.	71.8	-0.230 n.s.
Shallow samples vs. spawning-ground samples	-0.272 n.s.	16.8	-0.350 n.s.
Spawning-ground samples Male vs. female	0.852*	60.8	0.697 n.s.

* = significant at $P = 0.025$
n.s. = not significant
DML = dorsal mantle length

Figure 7. Comparison of prey frequency and number by sex of spawning-ground captured squid.

Figure 6. Comparison of prey frequency and number by depth of capture for non-spawning squid.

Prey Determination—Spawning Ground Males versus Females

Little difference was found between the feeding habits of male and female *L. opalescens* from the spawning grounds (Figure 7, Table 1). In both sexes crustacean feeding predominated, with mysids and megalops larvae being the primary foods. Juvenile gastropods also were important, with nereid polychaetes, and fish (juvenile *Sebastes* sp. and pleuronectiforms) playing lesser roles (Table 1). No whole-cephalopod feeding was found, although cephalopod fragments were ingested more often than off the spawning grounds. The miscellaneous category was dominated by egg-like spheres, but sand particles were also found.

The only major differences between sexes were in megalops larvae and cephalopod fragments (Figure 7). Male squid took cephalopod fragments more frequently and ate more megalops per meal than females. Females fed more on polychaetes, egg-like spheres, and cumaceans. A significant association between prey ranks was found in percent frequency of occurrence but not in percent by number of prey species, although the similarity index was relatively high (60.8%; Table 2).

Prey Determination—Spawning Grounds versus Shallow Water

A marked contrast was found in food items eaten by squid taken from spawning grounds compared to squid
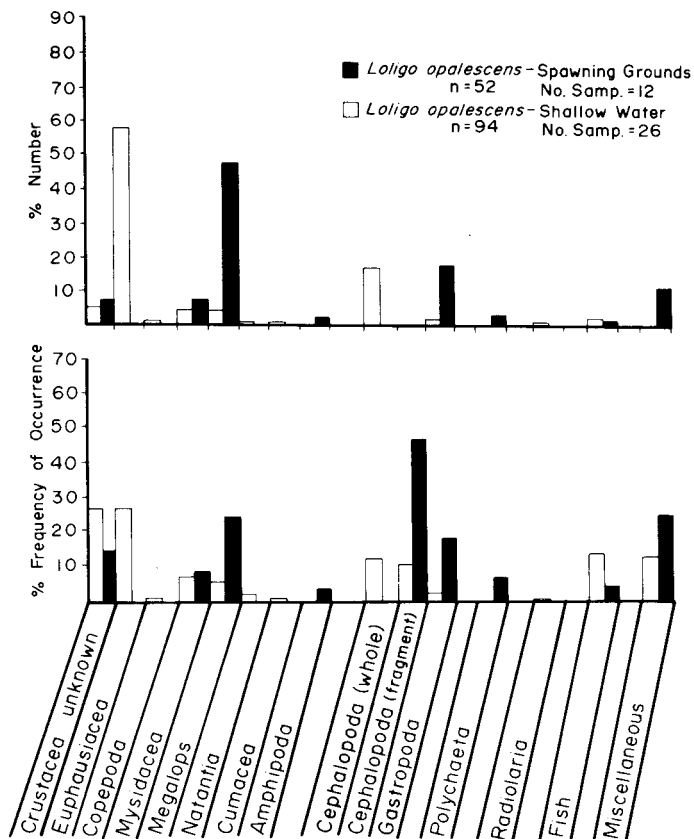
Figure 8. Comparison of prey frequency and number by location and depth of capture.

taken in near-surface waters (Figure 8, Table 1). On the spawning grounds, crustacean feeding still dominated, although of a different kind, with megalops larvae replacing euphausiids. Polychætes, juvenile gastropods, and egg-like spheres also became more common, replacing fish and whole cephalopods. Cephalopod fragments played a much larger role on the spawning grounds. A very low similarity index (16.8%) agreed well with the finding that no significant association occurred between prey ranks of spawning ground and shallow-water squid in either percent frequency of occurrence or percent by number of prey species. (Table 2).

DISCUSSION

Squid have been reported to change their feeding habits with growth in size. Squires (1957) described for the Newfoundland squid *Illex illecebrosus* a diet of mostly euphausiids in small animals (100- to 200-mm mantle length0, with fish in only 12% of the food-containing stomachs. In larger squid, the occurrence of crustacea declined to insignificance, with fish increasing in importance until they became the major component of the diet. Cannibalism increased among the largest animals

(250- to 300-mm mantle length).

Vovk (1972) reported a similar trend in the East Coast squid, *Loligo pealei*. Planktonic feeding was dominant in the smallest squid (75-mm mantle length). Euphausiid feeding became increasingly important to larger squid (125-mm mantle length). Cannibalism and fish feeding dominated in sizes larger than the 160-mm mantle length.

Kore and Joshi (1975), working with the Indian squid, *Loligo duvauceli*, reported a similar increase in cannibalism and decrease in crustacean feeding for larger squid. These were the only authors that distinguished true cannibalism from the ingestion of cephalopod fragments such as skin and tentacle fragments.

Fields (1965) also reported a similar trend for *L. opalescens* captured in Monterey Bay. His study was based on a sample of 75 animals subsampled from commercial fish seiners and 31 male squid from the spawning grounds. Only those squid whose stomachs appeared from external examination to have contents were used in his study. He reported a trend of crustacean to fish feeding of 3:1 in small squid, 1:1 for young squid, and 1:3 for adult squid (males from the spawning grounds). Fields stated that feeding on the spawning grounds was probably atypical because of the ground's localized nature and the increased crowding that the animals experienced. These spawning adults were reported to show 75% cannibalism in frequency of stomachs with contents. No distinction was made between true cannibalism and cephalopod fragments. In our study no spawning-ground animals were included in the comparison between sizes in order to avoid the localized nature of feeding on these grounds.

We found a closer correlation in feeding habits between different sizes of *L. opalescens* than was reported by Fields (1965). Certainly, there was a trend for larger animals to feed more on cephalopods and fish than the smaller sizes of squid, but significance of association by frequency of occurrence and a high percent similarity index does not support this trend. The possibility that other squid do show major differences in feeding habits between size categories can still be explained. Both *L. pealei* and *I. illecebrosus* are larger animals than *L. opalescens*. If feeding habits of sizes similar to *L. opalescens* are examined for these two species, crustacean feeding dominates. Another possible explanation is that, unlike our study, these authors did not separate location of capture from size of squid captured. Squires (1957) pointed out that *Illex* captured on the outer edge of the Grand Banks were also the smaller squid and were found to feed more on euphausiids than larger squid taken on the Grand Banks.

Our comparison by depth of capture could not clearly be separated from a comparison of location since the shallow water (less than 40 fathoms [73.2 mm]) was also

from the more inshore areas. It is, therefore, not clear if the greater amount of euphausiid and copepod feeding in deep-water samples resulted from increased availability in deeper waters, or offshore waters, or both. It does appear, however, that as reported by Squires (1957) for *Illex*, *L. opalescens* taken inshore had a different diet from those taken offshore.

Fields (1965) suggested that female *L. opalescens* do not actively feed on the spawning grounds. Our results indicate that females do feed on the spawning grounds, although perhaps less intensively than males. Only percent frequency of occurrence of prey items between spawning ground males and females was significantly associated, while percent by number was not. Males ate larger meals by number than females. Perhaps, as suggested by Fields (1965), female squid do have digestive tracts in less active condition than do males.

It became clear that spawning-ground feeding was indeed atypical, as suggested by Fields (1965), when these samples were compared to other areas at similar depths. The percent similarity index was lowest in this comparison, and no correlation was found in either percent by number or frequency of occurrence.

Demersal feeding was more important on the spawning grounds, with bottom-associated organisms such as megalops larvae, polychætes, gastropods, and eggs being more common in the diet. Crustacean feeding still dominated, with euphausiids being replaced by the more seasonal, and perhaps more localized, megalops larvae. Cephalopod fragments occurred most frequently in spawning-ground samples. True cannibalism, however, did not occur on these grounds. Cephalopod fragments probably do not reflect true feeding, but some form of behavior associated with crowding. This could explain the higher incidence of cephalopod fragments on the spawning grounds where animals tend to be more crowded.

Overall, it appears that *Loligo opalescens* is an important predator in the pelagic ecosystem of Monterey Bay, and presumably elsewhere in the California coastal waters. It feeds primarily on smaller crustaceans such as euphausiids, copepods, megalops larvae, mysids, and amphihpods but also utilizes larger prey items such as fish and other cephalopods. The diet of *L. opalescens* changes markedly with depth of water and location but does not differ much between size categories or sexes. This appears to indicate that market squid tend to utilize similar prey items regardless of sex or size, but that differences in prey utilization may result from changes in patches of available prey or different behavior of this predator at different locations.

ACKNOWLEDGMENTS

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AGE AND GROWTH OF THE MARKET SQUID, *LOLIGO OPALESCENS* BERRY, FROM STATOLITHS

JEROME D. SPRATT
Operations Research Branch
California Department of Fish and Game
2201 Garden Rd.
Monterey, CA 93940

ABSTRACT

Growth increments have been found in statoliths. Growth increments correlate best with daily growth in juveniles and monthly growth in animals over six months of age. Monthly length at age reveals that market squid spawn at 1 to 2 years of age and most spawn when 14 to 22 lunar months of age at about 100-145 mm dorsal mantle length.

INTRODUCTION

The California squid fishery is one of the state's oldest fisheries, dating back to the 1860's when Chinese began fishing in southern Monterey Bay. The fishery has evolved over the years into an industry with annual landings averaging 22 million pounds over the period 1966-75. Today, the market squid resource of California is still considered underutilized, and considerable expansion of the fishery is likely in order to meet the world's growing protein demands.

There is relatively little known about the life history or population dynamics of the market squid. The California Department of Fish and Game with Moss Landing Marine Laboratories have undertaken a Sea Grant Project to answer some of these questions, including growth rates.

Age and growth studies on squid, as a group, are very difficult. Few species have been taken in numbers large enough to allow any age and growth analysis. *Loligo opalescens* (Fields 1965), *Illex illecebrosis* (Squires 1966), and *Loligo pealei* (Summers 1971) have been aged by analyzing modal length frequencies collected through time. All of those researchers estimated age at maturity to be two or three years. In this type of an analysis, several assumptions must be made that cast some degree of doubt on the validity of results obtained. Absolute age is not known because the age of the smallest specimens collected must be estimated. Random sampling is difficult, and sampling probably introduces bias. And finally, movements or migrations of size classes make it extremely difficult to sample the same group or size class through its life span.

Tag and recovery studies on *Todarodes pacificus* (Otsuki and Araya 1958) show that this species reaches maturity in one year, spawns, and dies. Tag and recovery studies could be conducted on *Loligo opalescens*, but it would require a method of holding specimens while experimenting with methods of tagging. The technology for a study of this nature is not available at present.

La Roe (1971) successfully cultured the loliginid squid, *Sepioteuthis sepioidea*. This species grew to 105-mm mantle length in 146 days and was sexually mature. The technology to maintain juvenile and adult squid in long-term captivity studies is not available. If squid could be raised for long-term studies, the effects of an artificial environment on growth could not be defined and comparison with wild animals would be difficult.

Either the validity of the preceding methods is difficult to define, or the methods themselves are not applicable to *Loligo opalescens*. The purpose of this study is to develop another method of aging by examining the hard body parts of squid for evidence of growth marks that could be correlated with time. The body parts considered are the gladius, beaks, and statoliths. The gladius exhibits markings that could represent growth increments. A sagittal section of the gladius reveals that growth occurs in layers which could be correlated with time. Beaks of *Moroteuthis ingens* (Clarke 1965) were found to have growth lines, but the time it took to form growth rings could not be determined. I sectioned beaks of *Loligo opalescens* and found that they were formed in layers much as the gladius was.

A few statoliths were given to Dr. Edward Brothers (National Marine Fisheries Service, La Jolla), who found that statoliths of *Loligo opalescens* had many concentric growth rings much like otoliths.

It is my opinion that the gladius, beaks, and statoliths all are suitable for age and growth studies. However, I chose the statolith because of its similarity to the otolith.

This paper is concerned with a new method of aging squid, the techniques involved, and the validity of the results.

STUDY AREA

All the specimens of market squid used in this study were collected in Monterey Bay, California (Figure 1). Squid are available in this area year round; however, sampling is difficult in the winter months.

METHODS AND MATERIALS
Sampling

The initial phase of this study was concerned with examining modal length frequency progressions in order
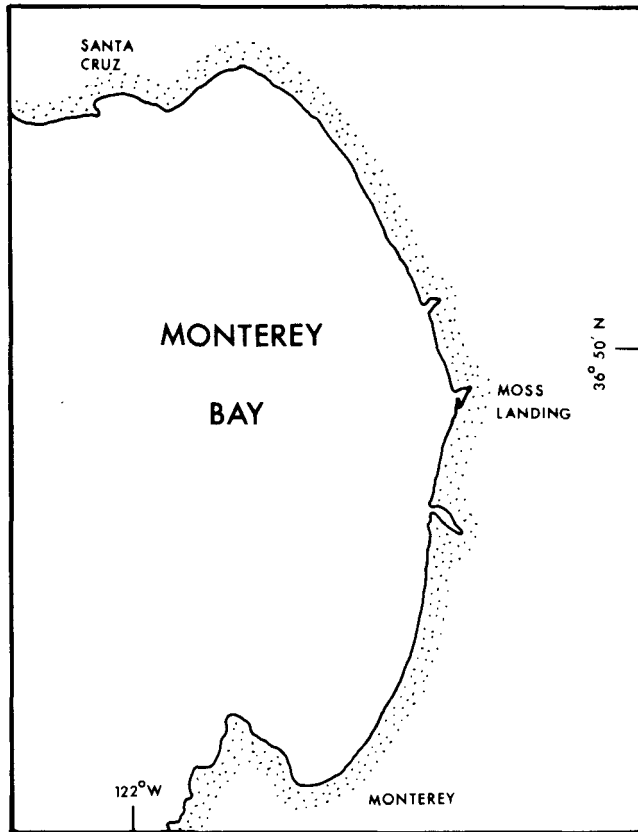
Figure 1. Study area.

to estimate growth. Length was recorded as dorsal mantle length (DML) in mm. The commercial catch was sampled for adult animals. The commercial squid fishery takes spawning adults with lampara nets and does not provide samples of immature animals.

Larval and juvenile squid were sampled as the opportunity presented itself. Most collections were by mid-water trawl from research vessels. Juvenile and adult squid are also present with purse seine-caught anchovies, and their occurrence there provided an additional source of squid during the fall and winter months.

Larval squid are present nearly year round from May to at least January, but peak hatching occurs June through August. Larvae were taken during this period, and young juveniles sampled from the winter anchovy catch were considered to be from the previous summer spawning period. By the following summer the earliest-hatched squid from the previous summer were large enough to appear with spawning schools and were taken in small amounts in the squid fishery.

Sampling of juveniles may be biased since a certain size could school with anchovies. However, sampling apparently reveals growth. The validity of the growth rate will be determined from growth increments in stato-

liths. Statoliths were taken from squid during normal sampling operations. Collecting statoliths was biased in the sense that statoliths were taken from all sizes of squid available.

Statolith Extraction and Preparation

Statolith Extraction

A dissecting microscope with magnification up to 40-50x is necessary to dissect larval-sized squid (<10 mm total length). Larger sizes required progressively less magnification, and adults over 100 mm DML do not require a microscope for dissection.

Statoliths are located just posterior and ventral to the eyes and are removed in the following manner. Begin with the ventral side up and remove the funnel apparatus. In large squid it may be ncessary to split the mantle in order to remove the funnel. In small squid (<75 mm DML) the two statoliths will be visible, appearing as white opaque objects lying side by side under a thin layer of transparent tissue and cartilage. In larger squid it is necessary to scrape the muscle tissue away with a scalpel until the ventral side of the cranial cartilage is exposed. The two visible statoliths can be removed with forceps after cutting the statocyst in half. The statoliths are not fragile but can be broken if handled roughly.

Cleaning and Storing

Generally statoliths require no cleaning, but any adhering tissue should be removed. They can be stored indefinitely in labeled gelatin capsules.

Embedding

Statoliths must be ground in order to see growth rings, and due to their small size, handling is much easier if they are embedded. A Fullum mold (Figure 2), which is reusable and has space for 24 statoliths, is used. The statolith must be placed on its side in the bottom of the mold so that it will be parallel with the plane of grinding. Any clear, fast-drying resin may be used and is poured over the statolith, filling the mold. The hardened resin block is a permanent mount and can be stored in labeled coin envelopes.

Grinding

The embedded statoliths should be just under and parallel to the surface of the resin block. Grinding is done on carborundum paper (200-600 grit) and must be done very slowly with frequent stops to check progress under a microscope. Polishing with aluminum oxide or diamond plate will help eliminate scratches in the statolith but is not necessary to view growth rings.

Viewing

A compound microscope with substage illumination was used to check the statolith during the grinding pro-

cedure and for viewing growth rings. Magnification of 400-600X is adequate for counting growth rings. Higher magnification up to 1500X does not reveal any more detail.

Reading Criteria

Growth Increments

When viewed under transmitted light, a growth increment is defined as the interface between an inner light and outer dark band. The market squid statoliths do not reveal annual growth increments. Growth increments change as the squid becomes older and can be grouped into two distinctive patterns.

Juvenile market squid form uniform, regularly spaced growth increments (Figure 3). Up to about 150 of these small, regularly spaced growth increments can be seen in juvenile market squid. These are considered to be near-daily growth increments. At about six months of age, growth increments change and become irregular in size and spacing, with large, prominent growth increments separated by usually five or six smaller ones (Figure 4). The larger growth increments are considered to form at monthly intervals. The validity of daily and monthly growth increments will be discussed later.

Counting Growth Increments

Two types of growth rings are visible in statoliths. An ocular micrometer is useful in counting the uniformly spaced rings in juvenile squid (Figure 3). At 450X with a 10-mm ocular micrometer, the growth ring widths nearly equal the graduations on the ocular micrometer. These first uniform rings are best seen from the nucleus to the posterior margin of the statolith (Figure 5). The larger rings formed later in life can be counted without any special techniques. On adult squid it is difficult to see the first uniformly spaced rings, and counting begins with the first larger ring formed, which is believed to be formed at about six months of age. The growth rings formed later in life are best seen on the rostrum (Figure 5).

RESULTS

Sampling of commercial squid landings, anchovy catches, and midwater trawling from 1972-1975 provided length-frequency data that indicated the market squid lives a maximum of two years (Figure 6). The spring brood grows rapidly during the summer months and is ready to spawn the following summer. The fall brood grows slowly until the next summer, when growth accelerates, and will spawn the next fall or spring.

The spawning season extends from April to December in Monterey Bay, but peaks in May-June and November-December. The long spawning season clouds length-frequency data because squid of all sizes are present at all times of the year and it is difficult to follow each brood as it matures.
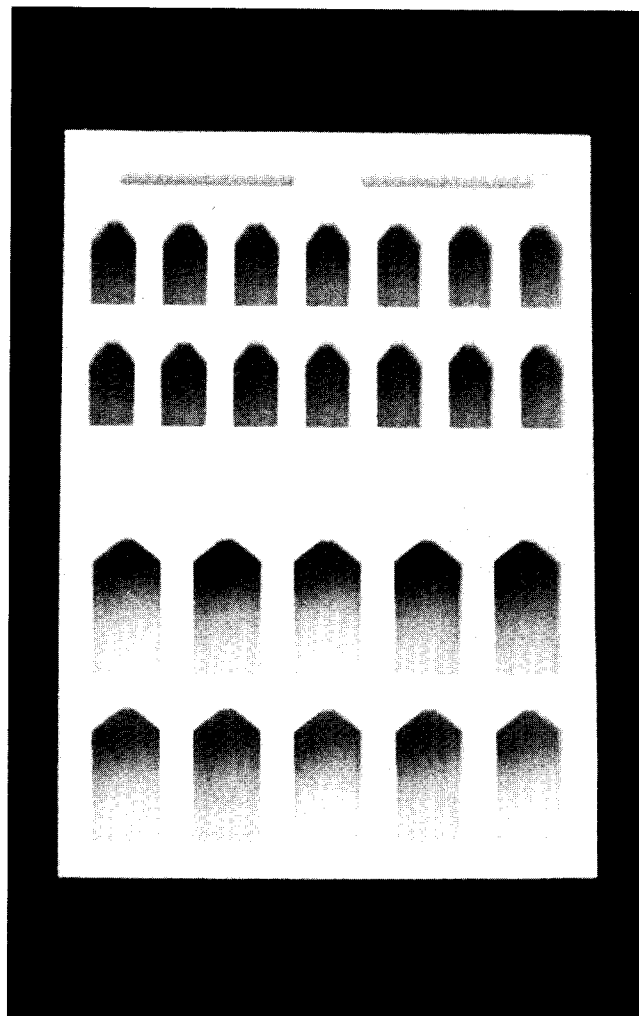
Figure 2. Fullum mold with space for 24 statoliths.

Fields (1965) analyzed modal length frequencies of market squid from Monterey Bay and concluded that most market squid spawn at three years of age but that some animals mature at 1, 2, and 4 years of age. His basic hypothesis is that the growth rate is constant and about 4 mm/month. This is unrealistic, since growth should be rapid initially and gradually slow as age progresses. Fields' results are at best hypothetical, and their validity has not been determined.

Fields and I disagree, but growth increments found in statoliths support my results that the market squid spawns at between 1 and 2 years of age.

I have aged 100 squid from statoliths. Age was assigned in months, based on the number of near-daily growth increments (Figure 3) and the number of proposed monthly increments (Figure 4). The maximum age recorded was 25 lunar months or almost 2 years. A growth curve was developed (Figure 6) which shows growth is rapid from spring to summer and slows during the winter. Squid mature at about 100 mm DML or at 14 months of
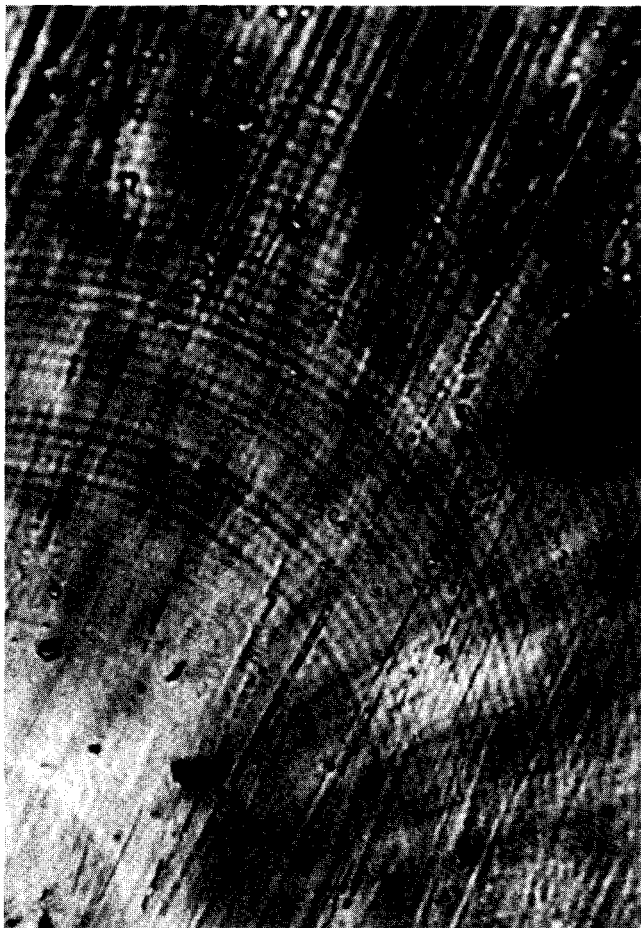
Figure 3. Small, regularly spaced growth rings formed during juvenile life stages.

Figure 4. Large, irregularly spaced growth rings formed during adult life stages.

age. During the spawning season the size range for most market squid is from 100 to 145 mm DML when they are 14-22 lunar months old. Squid up to 200 mm DML have lived through two growing periods (summers) before they spawn.

Validity

Conclusive evidence that the majority of market squid spawn at 1 to 1½ years of age is very elusive. However, the validity was tested by two independent methods, and both methods provide a measure of validity to my results.

Rearing

Ann Hurley, at Scripps Institution of Oceanography, attempted to raise market squid and was kind enough to provide me with squid of known age that could be aged from the statoliths. Unfortunately, she was unable to raise squid past 2 months of age. The growth rate of these squid is suspect because they were held in a near-starvation state due to the difficulty in providing proper food organisms. The squid that lived 2 months were only 4-5 DML or about 2 mm larger than when they hatched. I
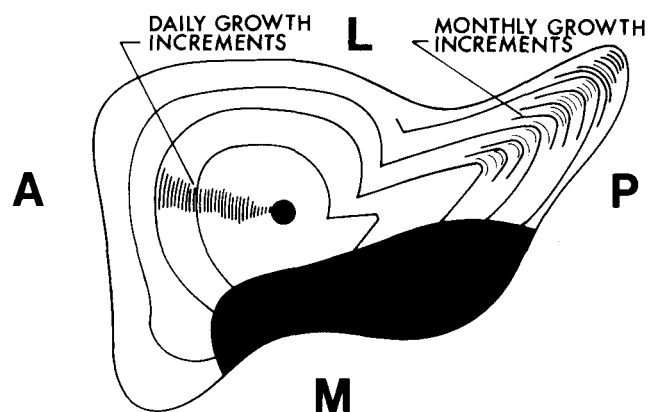
Figure 5. Ventral view of hypothetical statolith from an adult squid, as it appears under transmitted light. Anterior (A), posterior (P), median (M), and lateral (L) surfaces are labeled. Areas where daily and monthly growth increments are best viewed are indicated.

would expect a squid 2 months old to be 15-20 mm DML. The statoliths from Hurley's squid did have small, uniformly spaced growth increments. Growth increments were possible to count on six specimens, and counts were

61
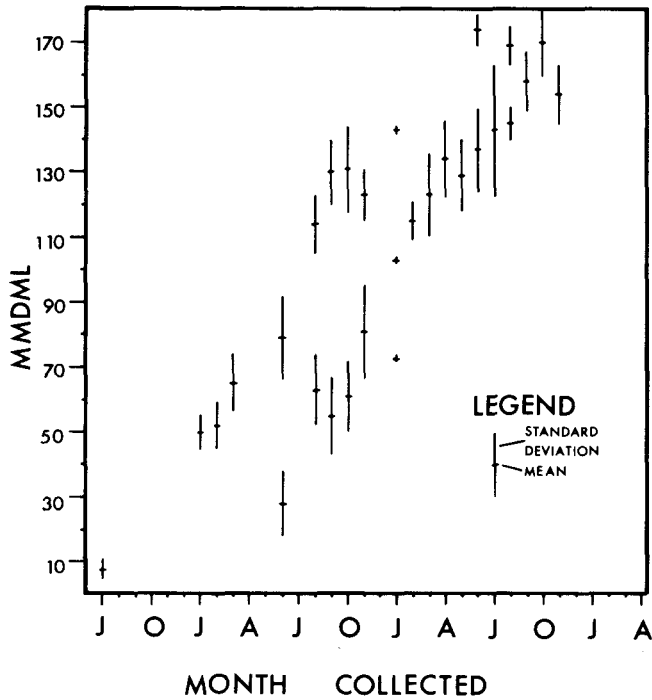
Figure 6. Modal size (mm dorsal mantle length) collected through time from 1972-1975.

Figure 7. Growth rate of market squid (mm dorsal mantle length) from statoliths.

TABLE 1

Number Growth Rings in Statoliths from Squid of Known Age.

Specimen	Age in days	Growth rings in statoliths
1	67-70	28
2	67-70	32
3	28-31	30
4	43-44	15
5	54-55	35
6	55-56	38

made without knowledge of age. One squid's age in days agreed exactly with the number of growth increments. However, the remaining five squid had significantly less growth increments than the days of age (Table 1); this could be due to the near-starvation situation. Hurley's study shows that growth increments are formed rapidly and can be formed at a daily rate. It is probable that a wild squid would grow much more rapidly and would form growth increments at a uniform, near-daily rate. This provides a measure of validity for designating the rate of formation of the first 150 growth increments as daily.

Time Series Samples and Estimated Growth Rate

The second method of validation was to compare my lunar-month growth rate (Figure 7) with the length modal

Figure 8. Market squid growth rates from statoliths compared with modal length (mm dorsal mantle length) progressions.

progressions that were collected previously (Figure 6). If length at age is superimposed on length frequencies (Figure 8), the results are very encouraging. The estimated growth rate fits the length modal progressions quite well. My growth rate is for summer-spawned squid, but squid also spawn in the fall. If my growth curve is

shifted six months to the right, very little adjustment is needed for it to pass through length modes not accounted for by the growth curve for summer-spawned squid and could represent growth of fall-spawned squid.

The fact that the majority of squid spawn in the spring and early summer could mask a probable different growth rate for fall-spawned squid. Assuming the squid I have aged are all early-summer spawners, the resulting growth rate agrees well with monthly length frequencies and lends another measure of validity to my results.

Growth Increment Formation

Squid are strongly phototaxic and are known to feed during daylight hours. This is the mechanism that causes the formation of daily growth increments. Contrasting growth increments are formed during daily feeding and resting actvities. At about 6 months of age, a change takes place in the type and rate of growth-increment formation. This could represent a transition phase in the squid's life history. Regardless of age, this size of squid is frequently taken mixed with anchovy schools, which have a strong diurnal movement pattern, and indicates that this size of squid is beginning to migrate into the deeper adult habitat. Why the growth-increment formation becomes irregular is not well understood. Prominent large growth increments are formed periodically, which have up to 5 or 6 smaller increments between them (Figur 4). Spawning adults have 6 to 18 of these prominent growth increments. This number of adult growth increments correlates best with lunar periods. A prominent growth increment could be formed during heavy feeding activity associated with full moon. Prey organisms with a diurnal pattern would be more available on moonlight nights. At any rate, the large prominent growth increments are considered to represent monthly growth.

DISCUSSION

Market squid reach a relatively small size (100-200 mm DML) by the time they spawn, and they spawn once and die. This knowledge coupled with the knowledge that other species of squid (*Todarodes pacificus* and *Sepioteuthis sepioidea*) reach adult size in one year or less, implies that market squid could grow at a rapid rate until spawning occurs. The modal length progressions and growth rings on statoliths support the hypothesis that market squid grow rapidly and are capable of reaching adult size in about 14 lunar months.

Upwelling normally begins about April in central California, and the added nutrients in nearshore areas cause plankton blooms during the summer. Plankton are the primary food source of young squid.

Market squid spawned early in the summer (April-May) will grow rapidly during the summer growing season and are capable of reaching adult size in about one year. As spawning continues from June through September, newly hatched squid will have progressively less time available in the growing season. This will have the effect of slowing the growth rate. During the next summer (growing season) this late-summer brood will increase in size and probably spawn from October to December at an age of 14-19 lunar months.

Late-fall-spawned squid (October-December) will grow slowly until late spring, when growth will accelerate. But it is likely that they will be beyond the plankton-feeding stage and will feed on small fishes or newly hatched squid. This will cause them to expend more energy capturing food items and could cause a slower growth rate. Some fall-spawned squid may reach adult size in one year, but I suspect most fall spawners must live through part of a second growing season before they spawn. The majority of squid spawned in October to December would most likely return to spawn in their second summer when about 18 to 22 lunar months old.

Squid have been aged up to nearly 2 years old, and those represent slow-growing squid that have lived through part of their second growing season. It appears that spring and fall spawning activities do not represent separate populations. An individual squid, depending on its growth rate, could return to spawn anytime between 1 and 2 years of age. The fall spawning activity is probably composed of squid that deviate from the normally expected growth rate; that is, they grow fast and spawn at an early age or grow slow and spawn at an older age.

CONCLUSION

Fields (1965) concluded that the market squid spawns at between 1 and 4 years of age and that most spawn at 3 years of age. The validity of Fields' conclusions was never determined.

Daily and monthly growth increments found in statoliths now support my results, which indicate that the market squid is capable of spawning at 1 year of age and that all will spawn during their second year of life.

A life span of 1 year has serious management implications. Spawning biomass can fluctuate dramatically from year to year because good recruitment is necessary each year to maintain the spawning population. A method of estimating recruitment should be developed. If fishing is not controlled during a year when poor recruitment is evident, spawning stocks could be reduced to a dangerous level.

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BEAKS OF THE MARKET SQUID, *LOLIGO OPALESCENS,* AS TOOLS FOR PREDATOR STUDIES

JERRY KASHIWADA AND CONRAD W. RECKSIEK
Moss Landing Marine Laboratories
P.O. Box 223, Moss Landing, CA 95039

KONSTANTIN A. KARPOV
The Resources Agency
California Department of Fish and Game
California State Fisheries Laboratory
350 Golden Shore, Long Beach, CA 90802

INTRODUCTION

Studies of feeding habits of predators are greatly complicated since digestive processes often leave prey items unrecognizable and unmeasurable. Items in such a state are of no value in determining the importance of prey species in the diet of the predator. Hard structures that resist digestion have allowed many researchers to identify and quantify prey items despite the deterioration of softer tissues.

Squid remains are found in the stomachs of many marine predators. Unfortunately, squid have few hard parts that resist digestion well enough to be used for stomach analyses. Dragovich and Wise (1969) chose to use the pen (gladius) for estimating body length and volume of ingested squid. The pen is not always a useful tool for stomach analyses of predators, since it can be easily fragmented and is seldom found intact. The chitinous beaks, however, are more resistant to fragmentation and are often found in the stomachs of predators. Beaks have proven to be valuable in many studies of cephalopod predators. Clarke (1962) used beaks to distinguish families and to estimate the weight of squid eaten by predators. He found that the lower beaks were more useful for identification. Clarke and MacLeod (1974) were able to distinguish species of cephalopods by various beak characteristics. The pictorial guide to cephalopod beaks developed by Iverson and Pinkas (1971) provides a method for distinguishing the beaks of *Loligo opalescens* from other squids found in the North Pacific Ocean. In addition to food habit information, Clarke and Stevens (1974) deduced possible migration patterns in blue sharks (*Prionace glauca*) by identifying the squid species eaten.

Although weights and volumes are essential measurements in feeding studies of specific predators, an estimate of body length is sufficient for our studies of the predators of *Loligo opalescens*. Spratt (1975) used a linear regression to estimate body size of northern anchovy (*Engraulis mordax*) from otolith measurements. A similar regression of dorsal mantle (body) length on beak dimensions could be used for estimating the size of *L. opalescens* from measurements of the beaks alone. Differences in sex, geographical location, and size may affect the accuracy of the estimates produced by regression. There is a noticeable difference in the size of the head and arms of males and females (Fields 1965). Clarke (1962) mentions possible differences in the amount of darkening of the beaks of the same species which are found in different geographical locations. The possible effects of these factors and their extent need to be examined. In this report we investigate the relationship between body size and various beak dimensions to develop a technique for estimating body sizes by measuring beaks of *L. opalescens* taken from predator stomachs. We also examine variability introduced by differences in size, sex, and geographical origin. We were especially interested in determining whether beak morphology could be used to detect the presence of subpopulations of *L. opalescens*.

METHODS

Loligo opalescens used for this study were captured in southern and central (Monterey Bay) California waters during a cruise of the California Department of Fish and Game research vessel *Alaska* (Cruise 76A4). Additional samples from the Monterey Bay area were taken from Moss Landing Marine Laboratories research vessel *Oconostota* cruises and from the catches of commercial fishermen.

The body of the squid was measured from the posterior tip to the anteriormost point of the mantle along the dorsal side (dorsal mantle length). The sex of the squid was recorded when such determination was possible. The buccal mass which contains the beak was extracted from a wide size range of squid from the two geographical locations. The beaks were extracted after the surrounding tissue was allowed to decay in a vial of water for a day or two. On each upper beak (Figure 1), four dimensions were measured: upper hood length (UHL), rostral darkening (URD), rostral length (URL), and rostral width (URW). Four measurements were also made on each lower beak (Figure 2): lower rostral darkening (LRD), hood length (LHL), crest length (LCL), and rostrum-wing length (LRW). Names of the beak structures were taken from Clarke (1962).

A dissecting microscope with an ocular micrometer was used to take the measurements. The measurements were plotted against dorsal mantle length (DML). Least square regressions of the measurements on dorsal mantle length were calculated (Sokal and Rohlf 1969, p. 410). Selected regressions were calculated for the beaks of Monterey Bay males, Monterey Bay females, southern California males, and southern California females. An
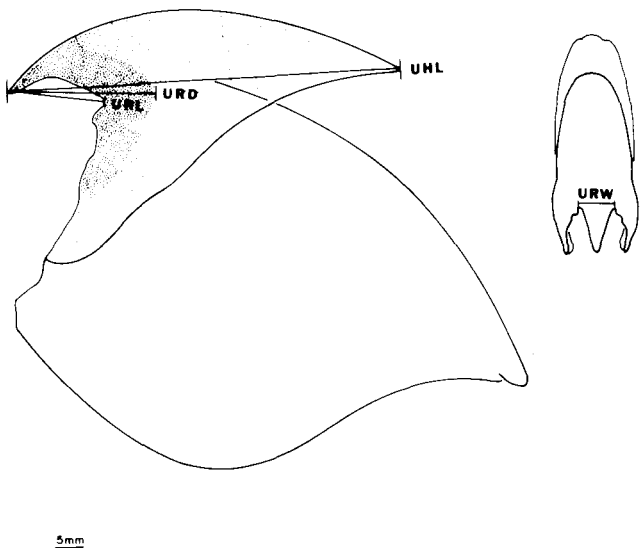
Figure 1. Illustration of upper beak showing the dimensions measured: URL (Upper Rostral Length), URD (Upper Rostral Darkening), UHL (Upper Hood Length), URW (Upper Rostral Width).
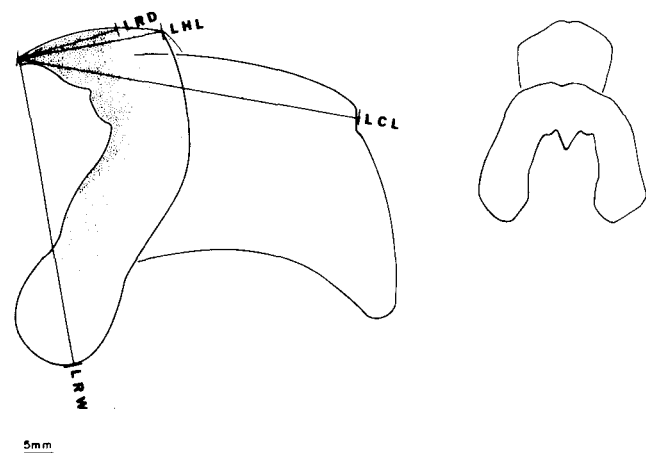
Figure 2. Illustration of lower beak showing dimensions measured: LRD (Lower Rostral Darkening), LHL (Lower Hood Length), LCL (Lower Crest Length), LRW (Lower Rostrum-Wing Length).

F-value was calculated to compare the significance of the regression lines (Sokal and Rohlf 1969, p. 420) of each dimension on dorsal mantle length for Monterey Bay males.

Differences in both sex and geographic origin were examined as sources of variation about the regression lines. To test for differences attributable to geographical location, the slopes and variances of the regression of upper hood length (UHL) on dorsal mantle length (DML) for Monterey Bay and southern California male squid were compared (Snedecor and Cochran 1967, p. 435). The same comparisons were made for Monterey Bay male and female squid to test for sexual differences.

In determining which beak dimensions would be most useful in predator studies, both the significance of the regression lines and the durability of the dimensions in resisting digestion were considered. The significance of the regression lines was compared by using the *F*-values mentioned above. One dimension was chosen for both the upper beak and lower beak. A regression of these dimensions on dorsal mantle length was calculated by combining all available data without regard to sex or geographical origin. Equations for estimating dorsal mantle length from measurements of these dimensions were calculated. Analysis of variance tables were calculated to allow the placement of confidence limits on estimates made from the equations. The slopes of the regression lines for southern and central (Monterey Bay) California squid were compared (Snedecor and Cochran 1967, p. 435) to determine whether separate regression lines for the two areas would be required for these beak dimensions.

The ratio of upper rostral length (URL) to upper rostral width (URW) was calculated to investigate possible proportional differences in size, sex, and geographical location. A 3-way analysis of variance was performed using a library computer program (Nie et al. 1975) to compare sources of variation attributable to these three effects. Three size groups, small (20-80 mm), medium (81-135 mm), and large (136-195 mm), were used. Central and southern California squid were used to test the effects of differences in geographical location.

RESULTS AND DISCUSSION

The calculated *F*-values show that the most significant regression lines for the upper and lower beak measurements are upper hood length (UHL) and lower crest length (LCL), respectively (Table 1). Upper rostral length (URL) and lower rostral darkening (LRD) had the least significant regression lines.

TABLE 1

Regression Statistics of Beak Dimensions (mm) on Dorsal Mantle Length (mm) for Male *Loligo opalescens* from Monterey Bay.

Beak Dimension	Regression Coefficient	Intercept	Error *df*	*F*
URL	0.0104	0.184	60	479.4
UHL	0.0481	0.243	58	2147.8
URW	0.0103	0.247	60	752.3
URD	0.0169	0.295	60	547.6
LHL	0.0178	0.212	60	645.1
LCL	0.0399	0.159	60	2096.1
LRW	0.0311	0.486	58	552.9
LRD	0.0124	-0.066	60	308.7

Since the slope of the regression lines is important in estimating body length from beak measurements, comparisons of slope and variance of the regression lines were made. The upper hood length dimension was chosen to test for differences due to geographical location because the high significance of its regression line makes it

more sensitive to possible differences. No significant differences in slopes and variances of the regressions were found. Since the slope of the regression line for southern California male squid is not significantly different from that for Monterey Bay male squid (Figure 3; Table 2), a single regression equation can be used to represent the relationship between upper hood length and dorsal mantle length for southern and central California *Loligo opalescens*. We believe similar comparisons of the other beak dimensions would also show no significant differences; these dimensions show more scattering about their regression lines and would be less sensitive in demonstrating differences in slopes.

TABLE 2

Comparison of Slopes of the Regressions of Upper Hood Length (mm) on Dorsal Mantle Length (mm) for Monterey Bay and Southern California Male *Loligo Opalescens*.

Location	df	B (Slope)	MSres
Monterey Bay...	59	0.0481	0.161
Southern California	53	0.0509	0.243

Comparison of slopes: $F = 2.17$ N.S.
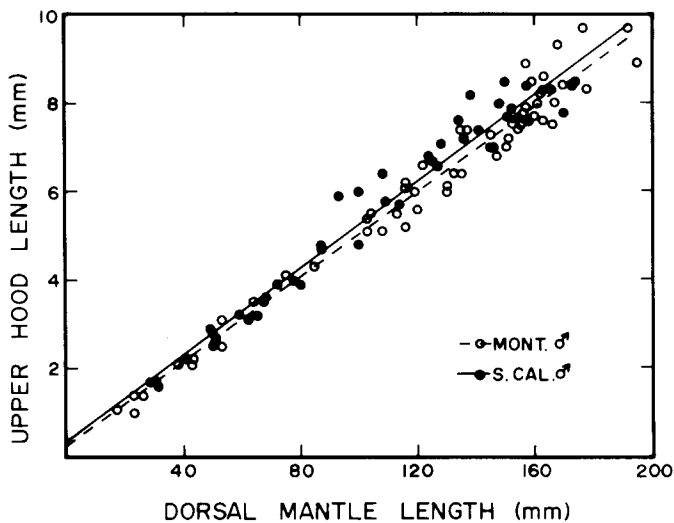
Figure 3. Regressions of upper hood length on dorsal mantle length for male *Loligo opalescens* from Monterey Bay and southern California.

No significant difference was found between the residual variances of the regressions of upper hood length on dorsal mantle length of central California male and female squid; however, a significant difference was found in the slopes of these regressions (Figure 4; Table 3). Although the difference was highly significant, it was not great enough to impair the usefulness of a regression line combining measurements of both males and females (*F*-values, Table 3).

The lower crest length and upper hood length dimensions would be the most useful dimensions for estimating the size of squid from beak measurements since they
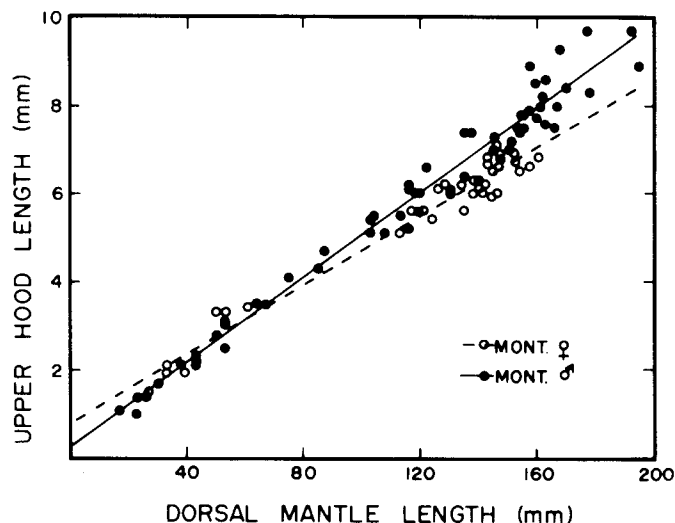
Figure 4. Regressions of upper hood length on dorsal mantle length for male and female *Loligo opalescens* from Monterey Bay.

TABLE 3

Comparison of Slopes of the Regressions of Upper Hood Length (mm) on Dorsal Mantle Length (mm) for Male and Female *Loligo opalescens* from Monterey Bay.

Sex	df	B (Slope)	MSres	F
Males	59	0.0481	0.1615	2147.8
Females	41	0.0393	0.0956	1417.1
Pooled ...	101	0.0451		2121.6

Comparison of slopes: $F = 32.0$ *** $(P < .001)$

exhibit the least scatter about their regression lines. Unfortunately, both these dimensions often cannot be measured because the beak structures involved are fragile and freqeuntly damaged. For beaks taken from the stomachs of predators captured in Monterey Bay, the lower hood length and upper rostral width dimensions were found to be the most durable (James Harvey, personal communication). Although the regressions for these two latter dimensions have more error, these dimensions are usually undamaged and are, therefore, more valuable as tools for stomach analysis.

All available data were used in plotting regressions of lower hood length and upper rostral width on dorsal mantle length (Figure 5 and 6). These dimensions did not show a significant difference between the regression lines for southern and central California *Loligo opalescens* (Tables 4 and 5). The combined regressions should therefore be useful for predator studies in both areas and presumably for the entire range of *L. opalescens*. To estimate dorsal mantle length from a given beak, regression analyses and analyses of variance for these two combined regression lines were performed (Tables 6 and 7). Confidence limits for estimates made from these equations can be calculated using a method described by Sokal and Rohlf (1969, p. 446).
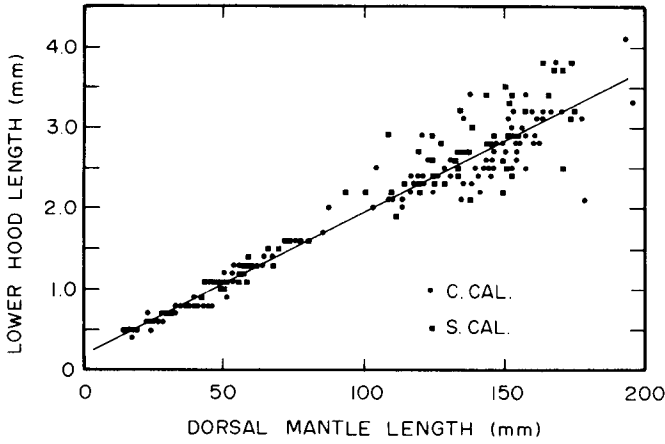
Figure 5. Regression of lower hood length on dorsal mantle length combining data for *Loligo opalescens* of both sexes and from both southern California and Monterey Bay.
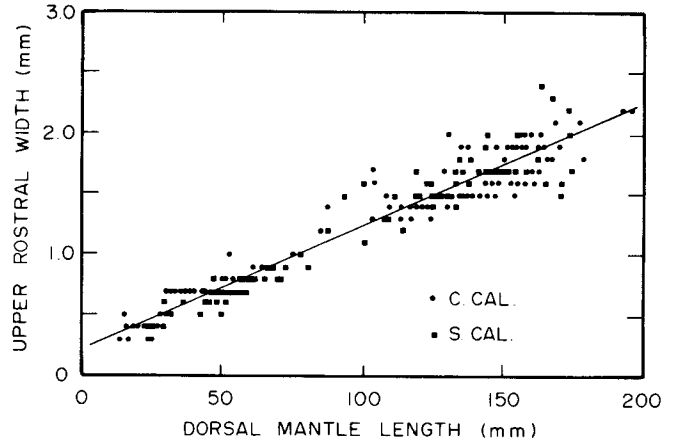
Figure 6. Regression of upper rostral width on dorsal mantle length combining data for *Loligo opalescens* of both sexes and from both southern California and Monterey Bay.

TABLE 4

Comparison of Slopes of the Regressions of Lower Hood Length (mm) on Dorsal Mantle Length (mm) for *L. opalescens* of Both Sexes from Monterey Bay and Southern California.

Location	df	B (Slope)	MSres
Monterey Bay ...	117	0.0169	0.0583
Southern California	96	0.0183	0.0705

Comparison of slopes: $F = 2.59$ N.S.

TABLE 5

Comparison of Slopes of the Regressions of Upper Rostral Width (mm) on Dorsal Mantle Length (mm) for *L. opalescens* of Both Sexes from Monterey Bay and Southern California.

Location	df	B (Slope)	MSres
Monterey Bay ...	117	0.0099	0.0187
Southern California	96	0.0107	0.0225

Comparison of slopes: $F = 3.76$ N.S.

TABLE 6

Regression Equation of Lower Hood Length (mm) on Dorsal Mantle Length (mm) and Analysis of Variance Table Combining Data for Both Sexes and Both Geographic Locations.

LHL = 0.01760 x DML + 0.21763

Source of Variation	df	SS	MS	F_s
Explained ...	1	164.015	164.015	2495.51
Unexplained	213	13.999	0.065723	
Total	214	178.014		

$y^2 = 178.014$
$x^2 = 528,614.321$
$xy = 9,311.31953$

TABLE 7

Regression Equation of Upper Rostral Width (mm) on Dorsal Mantle Length (mm) and Analysis of Variance Table Combining Data for Both Sexes and Both Geographic Locations.

URW = 0.01023 × DMP + 0.21648

Source of Variation	df	SS	MS	F_s
Explained ...	1	55.2338	55.2338	2674.11
Unexplained ..	213	4.3994	0.020655	
Total	214	59.6332		

$y^2 = 59.6332$
$x^2 = 527,473.953$
$xy = 5,397.63256$

TABLE 8

Model 1 Analysis of Variance Table for the Effects of Size, Geographic Location and Sex on the Upper Rostral Length/Upper Rostral Width Ratio.

Source of Variation	Sum of Squares	df	Mean Square	F	Significance of F
Main effects					
Size	0.43415	2	0.21707	13.848	0.001
Location	0.00001	1	0.00001	0.001	0.999
Sex	0.00013	1	0.00013	0.008	0.999
2-way interactions					
Size-Location...	0.01587	2	0.00793	0.506	0.999
Sex-Size	0.06981	2	0.03490	2.227	0.110
Location-sex ...	0.07413	1	0.07413	4.729	0.030
3-way interactions ..	0.08746	2	0.04373	2.790	0.064
Residual	1.88100	120	0.01567		
Total	2.56660				

The analysis of variance results for the upper rostral length (URL) / upper rostral width (URW) ratio (Table 8) shows there is a highly significant difference between the size of the squid, whereas no differences can be detected for sex or geographical location. The difference

is caused by an increase in the value of the ratio for the medium and large size groups. The 2-way treatment interaction of location and sex was significant at the .05 level (Table 8). The implications of this interaction are difficult to resolve since neither location nor sex was found to have a significant effect by itself. The interaction may have occurred because the squid in the Monterey Bay female small division were smaller than their southern California counterparts.

Aside from quantifying the relationships between body size and various beak dimensions, this research uncovered little evidence for variation in beak morphology with geographic location. Positive results in this area of investigation may have served as evidence for population- or climate-related differences. Our impression is that beak morphology by itself will not show such differences.

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Part III
SCIENTIFIC CONTRIBUTIONS

POPULATION ESTIMATES FOR THE WANING YEARS
OF THE PACIFIC SARDINE FISHERY

ALEC D. MACCALL
California Department of Fish and Game
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

New sardine (Sardinops sagax caerulea) population estimates for the period 1945 to 1965 are calculated based on a cohort analysis of aged landings data. Three-year-old fish were incompletely recruited after 1953, requiring assumption of age 4 as age of full recruitment. The assumed natural mortality rate (M) was maintained at 0.4 for the entire time series. Landings from waters south of Punta Baja, Baja California, were excluded from the analysis. Biomass estimates are smaller than those previously given but agree well with independent indices of abundance. The new ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one quarter to quadruple the estimated biomass. The stock-recruitment relationship shows no curvature for the entire time- series taken as a whole, and a purely functional description of the relationship is that mean recruitment only slightly exceeds potential replacement of spawners at all levels of abundance. Population simulations demonstrate this lack of resilience to fishing. Maximum constant fishing pressure that the population could have sustained was about 22% per year ($F = 0.25$). Maximum sustainable yield was about 250,000 tons/year, which is far below previous estimates.

INTRODUCTION

Estimates of Pacific sardine (Sardinops sagax caerulea) spawning biomass in California waters for the period 1932 to 1957 were made by Murphy (1966) using cohort analysis. Besides being the basis of most present analyses of the dynamics of the sardine fishery, estimates of spawning biomass from 1951 to 1957 have been used to calibrate larva surveys for estimation of northern anchovy (Engraulis mordax) spawning biomass (Smith 1972). As the northern anchovy fishery is now beginning to expand to a level where increased precision in management is necessary, improvement of the anchovy data base is desirable, and therefore, improvement of the sardine population estimates is indicated.

Murphy offered his analysis of the 1952-1960 seasons as a tentative solution and intended that "As more information . . . becomes available, the solution . . . can be re-examined." The last season for which the age composition of the sardine landings was published is 1965, which was also the last year of significant landings in California.

Murphy used landings up to 1960, so the usable time series can be extended another five years by updating his analysis. Other aspects of Murphy's analysis can also bear revision, particularly with regard to the present use of the results, that of anchovy biomass estimation. Murphy showed that a natural mortality rate of $M = 0.4$ is our best estimate, but for the time series subsequent to 1950, he preferred to double this value to $M = 0.8$ in order to obtain a trend in population sizes which agreed with the egg counts obtained from CalCOFI surveys. Since we are now using Murphy's estimates to calibrate those surveys, the process is suspiciously circular, and consistent use of the best estimate of $M = 0.4$ will preserve independence of the data sets. Age of full recruitment is another assumption that can bear examination and possible revision. Finally, Murphy included the Cedros Island catch in his landings data, which undoubtedly included large amounts of fish from the southern sardine stock that may never have been available in California. Since the northern anchovy central subpopulation has a southern boundary in the vicinity of Punta Baja, Baja California, estimation of biomass by comparing anchovy and sardine spawning products requires that the sardine biomass estimates be based on a similar area. Only sardine landings presumably caught north of Punta Baja will be considered in this analysis.

DATA

The basic input data to a cohort analysis are aged landings (Table 1). For the seasons before 1951, the catch data in Murphy's Table 13 are used. For the period 1951 to 1960, aged landings were recalculated from information in Wolf (1961) and from estimates of total tonnages landed in various regions of the fishery (Table 1). Age compositions for the 1961 to 1965 season were obtained from the individual landings reports (Daugherty and Wolf 1964; Kimura and Blunt 1967; Blunt and Kimura 1966; Kimura and Blunt 1971; Blunt and Kimura 1971; listed in order). Aged landings for each region were modified according to revised total tonnages obtained from various sources. In the late 1950's and early 1960's, sardine catches made out of season (i.e. in the "interseason") were not included in the landings reports, so aged landings were increased according to the tonnages reported in the California Department of Fish and Game Marine Fish Catch Reports. The aged landings for 1965-

TABLE 1
Pacific Sardine Landings.

Season	Landings (short tons)				Aged landings (1,000 fish)						
	Central California	Southern California	North Baja California	Total	O	I	II	III	IV	V+	Total
1950-51*	46,426	306,662	–	353,088			1,129,439	996,899	391,172	90,704	2,608,214
1951	15,679	113,125	16,022	144,826		13,908	69,624	778,877	179,837	79,603	1,121,849
1952	49	5,662	7,971	13,682		871	4,604	20,533	50,771	17,020	93,799
1953	58	4,434	12,303	16,795		2,150	5,928	35,025	10,812	49,606	103,521
1954	856	67,609	11,694	80,159	3,833	3,011	203,058	228,849	72,644	113,525	624,920
1955	518	73,943	3,828	78,289		11,340	71,827	268,656	140,996	57,483	550,302
1956	63	33,580	12,290	45,933			20,080	90,154	115,587	41,410	267,231
1957	17	22,255	8,932	31,204	4,393	56,544	57,910	77,527	35,141	41,120	272,635
1958	24,701	79,270	16,527	120,498		131,713	812,293	252,062	37,556	23,653	1,257,277
1959	15,645	21,538	14,140	51,323		67,723	299,484	150,980	18,231	2,112	538,530
1960	2,076	26,690	10,148	38,914		3,523	107,991	164,380	56,161	4,457	336,512
1961	2,211	23,313	1,587	27,111	1	369	11,029	34,613	76,001	45,837	167,850
1962	1,206	2,897	2,592	6,695		6	2,290	13,814	15,827	10,608	42,545
1963	1,008	2,459	2,521	5,988		1,458	4,332	9,202	13,291	11,347	39,630
1964	307	5,984	476	6,767	98	274	7,591	21,838	12,442	10,631	52,874
1965	70	909	431	1,410			730	523	2,250	4,765	8,268

*Landings prior to 1950 are as reported in Murphy (1966).

66 were poorly sampled and incomplete; therefore for this season the southern California age composition was assigned to all California landings and the Baja California interseason age composition was assigned to all Baja California landings. The amount of fish caught in northern Baja California waters before 1961 was estimated by multiplying the Baja California tonnage by the combined Ensenada and San Quintin percents of total landings in Murphy's Table 7. For 1961 through 1963, Murphy's Table 8 was used in similar fashion. The 1964 and 1965 landings reports say that "insignificant" amounts of the sardines processed in Ensenada were caught locally, which I have interpreted as 10%, for lack of a better estimate.

In most of the aged landings reports, no distinction is made between Cedros Island-area catch and Ensenada-area catch, which becomes a problem in 1961 through 1965, when large amounts of fish caught in central Baja California were shipped to Ensenada for processing and appear in the Ensenada landings estimates. Length frequencies for the two areas differ considerably in some years, with Ensenada fish being generally smaller than southern California fish and with Cedros Island fish being smaller yet (Blunt and Kimura 1966; Kimura and Blunt 1967). Two sets of landings data for 1961 to 1965 were analyzed separately, one assigning the Baja California age composition to the Ensenada catch, and the second assigning the southern California age composition to the Ensenada catch. As the true Ensenada age composition is likely to be intermediate between the two estimates, the estimates made by separate cohort analyses should correspondingly bracket the estimate that would have been obtained using the true Ensenada age composition.

ESTIMATION OF FISHING MORTALITY RATES

Cohort analysis, as described by Tomlinson (1970), was used to estimate fishing mortality rates from the aged landings data. Natural mortality is assumed to be $M = 0.4$, based on the review of sardine natural mortality rate given by Murphy (1966). Age 4 and older fish are considered fully recruited, so catch ratios of the form

$$R_i = \sum_{j=5}^{\infty} C_{i+1,j} \bigg/ \sum_{j=4}^{\infty} C_{i,j}$$

where i is fishing season, and j is age, were used to connect the time series of fully recruited ages. A backward solution estimated F_i, given F_{i+1} and R_i, and due to the assumption of full recruitment, the F_i so estimated for age-4+ fish was assigned to the age-5+ fish in the same season, allowing the process to be repeated for the next earlier cohort. The assumption of full recruitment at age 4 was necessitated by that being the oldest age for which older fish were still sufficiently abundant to obtain catch ratios that were relatively unaffected by sampling variation. Solution for the younger, partially recruited ages was also done by the method described by Tomlinson (1970). Murphy's solutions were based on mathematically equivalent calculations; therefore, the method itself is not a source of difference in the results given here.

The fishing mortality rate for fully recruited ages in 1965 was arbitrarily set at $F_{1965} = 0.6$ to initiate the time series. Since this is purely a guess, the 1965 and 1964 values must be considered inaccurate. Fortunately, backward solution has the property of convergence (Tomlinson 1970; Jones 1961), wherein each successive earlier estimate is less affected by error in later estimates and tends toward a fixed value, which can be called its

true value if all assumptions are valid. Thus, the F_i estimates for $i = 1963$ and earlier may be considered to be reasonably independent of the initial guess.

For the 1950's, fishing mortality rates estimated from the new data and assumptions tend to be two to three times larger than those estimated by Murphy (Table 2). After 1953, 3-year-old fish are not fully recruited, averaging 69% the fishing mortality rate of older fish from 1954 to 1963. Violation of the assumption of full recruitment caused progressive underestimation of F for "fully recruited" ages in Murphy's solution. This also explains why Murphy had to choose an inordinately large value of M and of F_{1960} to initiate his solution. The present solution gives results back to 1945, where the recalculation converges with Murphy's solution. Both previously discussed methods of assigning age composition to the later Mexican catches give approximately the same results (Table 2), except for the younger ages after 1961.

An additional factor tending to keep Murphy's estimates of fishing mortality low is his inclusion of catches from the more lightly exploited southern stock in central Baja California. As these southern landings become an increasing fraction of the total catch, the age composition of the southern stock, which reflects less fishing mortality, progressively dominates the cohort analysis, producing underestimated F and overestimated population size for the northern fishery.

ESTIMATION OF BIOMASS

Murphy's (1966) procedure was followed as much as possible, but information on actual weights of individual age groups in the catch compositions is lacking, forcing the use of approximate methods. Since total catch weight and landings by age in number are known (Table 1), age groups were assigned the weights at age given in Murphy's Table 17, and the total catch weight was apportioned by the estimated percentage weight composition, giving estimated landings by age in tons. These landings were then divided by the exploitation rate to give age group biomasses at the beginning of the season. Population biomass was then obtained by summing over age groups (Table 3). Murphy's calculations of spawning biomass for years before 1951 included only half of the 2-year-old fish. The present estimates include all of this age group for the entire time series, under the assumption that 2-year-olds are inherently capable of spawning and therefore constitute a "potential" spawning biomass. This simplification avoids the abrupt change of methods found in the previous estimates. Too little information is available to attempt to define a population size-dependent maturity function.

TABLE 2
Pacific Sardine Fishing Mortality Rates.

Age Season	$M = 0.4$			Murphy (1966) $M = 0.4$		Murphy (1966) $M = 0.8$	
	2	3	4+	2	3+	2	3+
1945-46	0.631	1.017	1.179	0.553	1.170		
1946...	0.496	0.752	0.595	0.476	0.589		
1947...	0.285	0.415	0.628	0.194	0.389		
1948...	0.314	0.313	0.326	0.346	0.192		
1949...	0.514	0.669	1.054	0.430	0.619		
1950...	0.455	1.148	1.207	0.394	0.796		
1951...	0.349	0.880	0.876		0.681	0.039*	
1952...	0.014	0.204	0.151		0.113	0.002	0.036
1953...	0.007	0.179	0.196		0.143	0.000	0.042
1954...	0.229	0.555	0.901		0.340	0.103	0.245
1955...	0.257	0.691	1.108		0.203	0.118	0.376
1956...	0.096	0.773	1.002			0.044	0.431
1957...	0.127	0.841	1.113			0.014	0.476
			(1.112)†				
1958...	0.922	1.790	2.424			0.690	1.218
	(0.916)	(1.783)	(2.417)				
1959...	0.503	0.553	0.808			0.406	0.783
	(0.501)	(0.546)	(0.798)				
1960...	0.592	0.756	0.528				1.359
	(0.565)	(0.752)	(0.516)				
1961...	0.128	0.490	1.440				
	(0.086)	(0.388)	(1.465)				
1962...	0.038	0.292	0.562				
	(0.002)	(0.358)	(0.445)				
	(0.149)	(0.079)	(0.683)				
1964...	1.549	1.353	0.896				
	(2.145)	(1.739)	(0.932)				
1965...		0.5	0.6				

*Estimated from Murphy's (1966) Tables 13 and 14.
†Parentheses indicate results of assigning southern California age composition to the Mexican landings in seasons 1962 through 1965.

TABLE 3
Pacific Sardine Biomass and Recruitments.

Year	Adult biomass (10^3 metric tons) Age 2+		Recruitment Year-class at age 2 (10^6 fiosh)	
	Present calculation	Murphy's (1966) Table 15	Present calculation	Murphy's (1966) Table 14
1945........	720	757	2,385	2,620
1946........	566	459	1,625	1,680
1947........	405	475	1,667	2,349
1948........	740	623	3,875	3,102
1949........	793	869	4,261	4,921
1950........	780	883	3,690	4,151
1951........	277	517	290	2,205
1952........	136	503	397	2,494
1953........	202	643	972	3,380
1954........	239	606	1,197	3,011
1955........	170	386	382	935
1956........	108	266	264	695
1957........	90	192	588*	1,216
1958........	177	255	1,586*	2,490
1959........	122	172	905*	1,327
1960........	88		288	
1961........	54		111	
1962........	27		74	
1963........	21		56	
1964........	11		11	
1965........	3			

*These recruitments are slightly underestimated due to significant catch of fish at age 1.

Biomass estimates for 1951 and later are much smaller than those calculated by Murphy, as is consistent with the estimates of fishing mortality rate. Despite the poor accuracy of the estimates of fishing mortality rate in 1964 and 1965, the biomasses for those years are undoubtedly extremely small relative to previous years. The two methods of assigning age composition to Mexican landings give nearly identical estimates of biomass, so the solution using Mexican age compositions is presented as the final estimate.

DISCUSSION

Availability at Age

As discussed earlier, Murphy's estimates of fishing mortality rates for the 1950's appear to have been biased downward because he included incompletely available 3-year-old fish in his catch ratios for assumed fully recruited age groups. Thus, the new estimates of fishing mortality rates that are based on an older assumed age of full recruitment are considerably higher because most of the catch ratios are smaller (i.e. catches of year-classes show a larger relative decrease in subsequent years). A comparison of relative availability to the fishery, as measured by the ratio of fishing mortality of ages 2 and 3 fish to "fully recruited" age 4+ fish (Figure 1) shows an interesting trend. Until 1953, 3-year-old fish appear to have been nearly fully available. This group subsequently, with the exception of the 1960 season, underwent a decline in relative availability to 70% in the later 1950's and to less than 50% in the early 1960's. Two-year-old fish show an even more severe drop in relative availability, a decline which also started earlier. From an average of 65% relative availability in the late 1940's, 2-year-olds dropped to 10% relative availability in the 1950's and later, with the exception of the warm-water years, 1958-60.

These trends are remarkably consistent with Felin's (1954) hypothesis concerning the geographic origin of year classes in the later years of the fishery, wherein the later, weaker year classes were thought to be of southerly origin. Now we can further hypothesize that as the fish in the catch were becoming predominantly of southern origin, slow rates of migration into California waters resulted in these fish not being fully available until an older age than was experienced from previous locally produced year classes. Oceanic conditions appear to have influenced this immigration rate as in the case of the warm-water years, when strong northward migration of sardines resulted in greatly increased availability of young fish to the southern California fishery.

Egg and larva surveys have shown little spawning in the Los Angeles Bight since 1951, except during the warm-water years (Kramer 1970). This independent
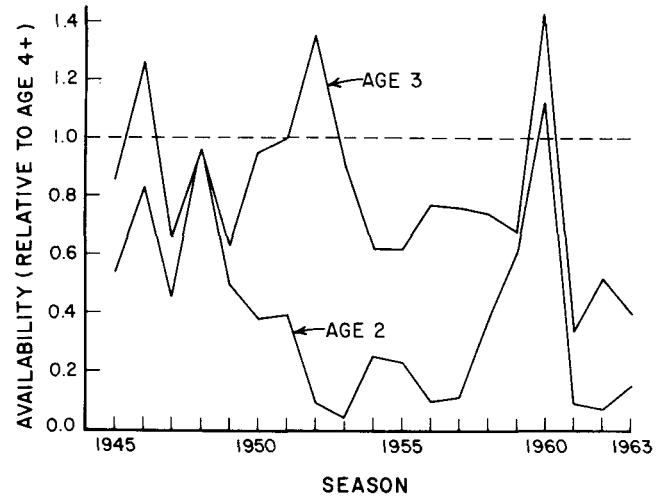
Figure 1. Relative availability of 2- and 3-year-old sardines compared to fully recruited age groups.

source of information strongly supports the above hypothesis, and the occurrence of northerly spawning in the warm-water years also helps explain the high availability of the 1957 and 1958 year classes. At the same time, these conditions of high availability resulted in the fleet generating maximal fishing mortality during this period, with the exploitation rate reaching 80% of fully recruited fish in 1958. It is ironic that the conditions that allowed the fishermen to rejoice at the return of the sardine insured the loss of the fishery by making those same sardines extraordinarily vulnerable to capture.

Biomass

Whereas Murphy's estimates of total biomass (age 2+) show a relatively large population in 1950, dropping to intermediate levels in 1951-1954 and then declining steeply, the present solution shows an extreme drop in biomass after 1950, and a subsequent slower, fluctuating decline (Figure 2). Of course, it must be emphasized that there is a geographic difference between the two population estimates in that the new solution is restricted to the waters north of Punta Baja, approximately the boundary between central and northern Baja California, and that much of the difference in the two solutions may be explainable on this basis alone. However, for examining events in the California fishery, the new solution should be more approriate. The decline since 1950 has been monitored by three other independent methods, and a comparison of these time series with both Murphy's and the new cohort analysis should be informative. The three independent methods are 1) catch-per-unit-effort (Clark 1956; Klingbeil 1974); 2) night-light surveys carried on by the California Department of Fish and Game (Klingbeil 1974); and 3) egg and larva surveys carried on by CalCOFI.

Figure 2. Comparison of sardine biomass estimates and indices of abundance.

Figure 3. Relationship between sardine spawning biomass and CalCOFI sardine larva census (from Smith 1972).

Catch-per-unit-effort (CPUE) indices of abundance, particularly when as unrefined as those used in the Pacific sardine fishery, are plagued with systematic errors. MacCall (1976) has shown that the catchability coefficient for available measures of effort in the earlier Pacific sardine fishery tended to vary inversely with biomass, causing decreased sensitivity of CPUE to changes in biomass. Knaggs (1972) documents a wide range of gear improvements in the fishing fleet since 1952. Most of the improvements were in relation to speed and efficiency in the capture and loading of fish. The Puretic power block reduced manpower requirements and ope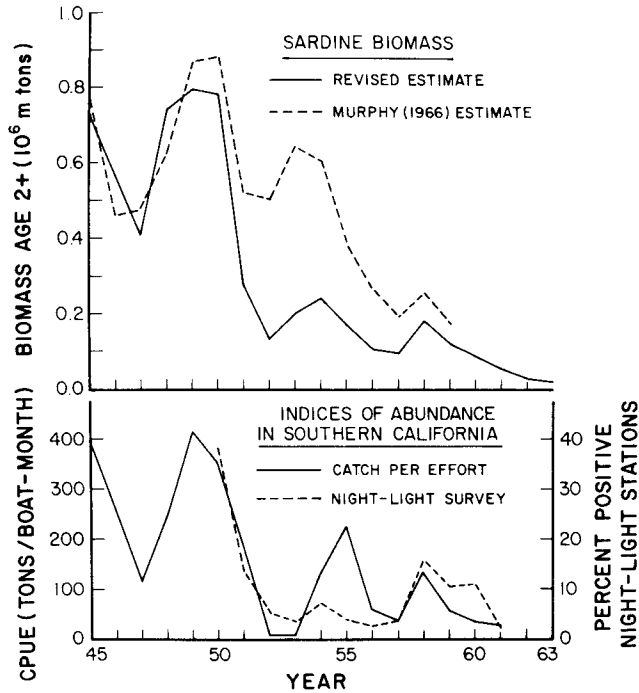rating costs and greatly decreased the duration of a set, allowing more sets to be made on smaller schools. Other improvements resulted in more efficient navigation and location of fish, such as aerial scouting, which takes most of the randomness out of the process of fish location and causes a tendency toward constant CPUE, independent of true abundance. Thus, while CPUE is likely to vary with abundance, it is also likely to underestimate changes in true abundance.

Since most of the landings occurred in the first months of the fishery season after 1944, it is reasonable to compare CPUE with biomass estimates for the beginning of the season. CPUE, in tons per boat-month as given by Clark (1956), and by Klingbeil's (1974) "first approach" (Figure 2), appears to agree somewhat more with the new

biomass estimates than with Murphy's estimates. The correspondence is good up to 1952, and the new estimates are much more consistent with the magnitude of the drop in CPUE from 1950 to 1952. The 1953 and 1954 seasons' CPUE are anomalous for both estimates of biomass, although the low fishing mortality rate supports the hypothesis that the stock was not fully available to the fishery. CPUE again agrees well with the new biomass estimates after 1954.

Klingbeil (1974) gives percentage occurrence of sardines at night-light stations as a tentative index of abundance. The index is based on a binomial distribution when fish are abundant, assuming the probability of getting a positive observation is directly related to abundance. However, as abundance becomes small, the probability of obtaining positive observations becomes small, and the distribution becomes approximately Poisson ($N > 100$ and $p < 0.05$), which has the property that the variance is equal to the mean. Thus, the relative precision is poor at low population sizes. Also, pre-recruits accounted for a large number of positive observations, so comparison with abundance estimates is very crude (Figure 2).

Other sources of bias in the night-light index are probable variations in fish behavior, both seasonally and annually. It appears likely that the same factors that may have caused exceptionally high availability of the popula-
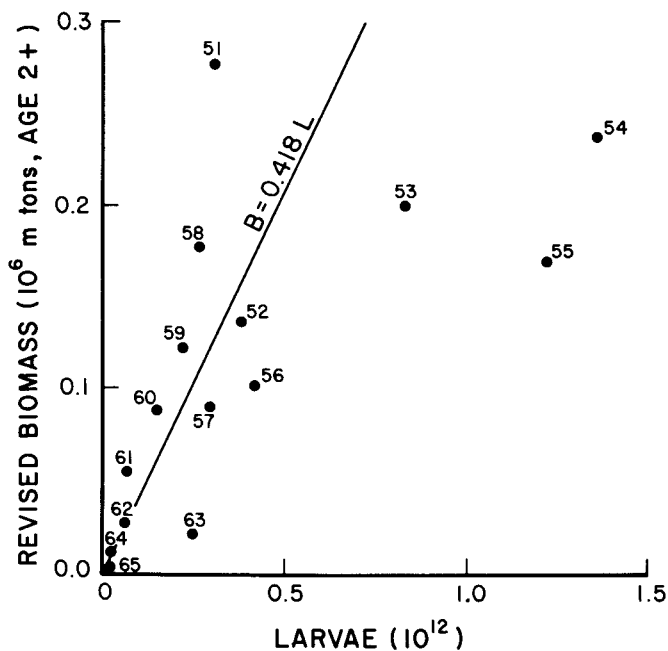
Figure 4. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census for area north of Punta Baja.

Table 4
CalCOFI Census of Pacific Sardine Larvae.

Year	TOTAL AREA (Smith 1972)		NORTH OF 30° N (Smith, personal communication)	
	census (10^9 larvae)*	biomass/larva (10^{-6} tons/larva)	census (10^9 larvae)	biomass/larva (10^{-6} tons/larva)
1951........	2685	0.193	305	0.908
1952........	2633	0.191	382	0.356
1953........	2189	0.294	732	0.276
1954........	3193	0.190	1361	0.176
1955........	1959	0.197	1220	0.139
1956........	1706	0.156	419	0.258
1957........	1137	0.168	293	0.307
1958........	1453	0.175	266	0.665
1959........	570	0.302	219	0.557
1960........	975		150	0.587
1961........	642		67	0.806
1962........	731		64	0.422
1963........	379		248	0.085
1964........	505		20	0.550
1965........	1098		19	0.179
1966........	735		31	
mean		0.207		0.418
standard deviation		0.053		0.251

*Smith (1972) erroneously used units of 10^{12} larvae.

tion to the fishing fleet in the warm-water years of 1958-1960 may have resulted in upward bias of the night-light index for those years. Nonetheless, the night-light index shows a large population in 1950, followed by a sharp decline. The 1951, 1954, and 1958 points suggest that abundance in these years may have been on the order of one-third that of 1950, which is much more consistent with the new biomass solution than with the old.

Smith (1972) used the relationship between Murphy's (1966) sardine biomass estimates and the CalCOFI sardine larva censuses to calibrate the CalCOFI anchovy larva censuses. However, Murphy forced his cohort analysis results to agree with the CalCOFI sardine egg censuses, which are highly correlated with the sardine larva censuses. Therefore, the remarkably good relationship between Murphy's estimates and the CalCOFI sardine larva censuses (Figure 3) is somewhat artificial and is not a test of the validity of his biomass estimates. Actually, the relationship is much tighter than should be expected: Taft's (1960) analysis of CalCOFI sardine egg sampling indicated that the variance of a single cruise estimate increases with the mean, so that 95% confidence limits for the mean would be one-half to double the estimated value. Since temporal variability is also extreme, the season estimate is probably relatively less precise than single cruise estimates. Also, in comparing spawning products with cohort analysis abundance estimates, further variability is likely from environmental influences

on spawning rates. Figure 3 shows none of these properties.

Although the recalculated sardine spawning biomasses are much lower than Murphy's for the period since 1950, the geographical area is also much smaller. For proper comparison, the CalCOFI censuses must also reflect this change in area, and therefore will also be considerably smaller than the previous values (Table 4). The revised relationship between larva censuses and estimated spawning biomass (Figure 4) shows much more scatter than did Smith's (1972) relationship; however, the pattern is very consistent with the sampling properties described by Taft (1960). When the logarithms of the variates are considered (Figure 5), the geometric mean (GM) regression (Ricker, 1973) slope is 0.973. This slope is reasonably close to the value of 1.0, which is characteristic of a proportional relationship between the untransformed variates and is a necessary quality of a good index. The error variance is constant for the log transformation, and the scatter about the regression is about twice Taft's "one-half to double" $s = 0.691$, 95% confidence limits are one-quarter to quadruple.)

Smith (1972) found the relationship

$$B = 0.206 \, L \quad (s = 0.053)$$

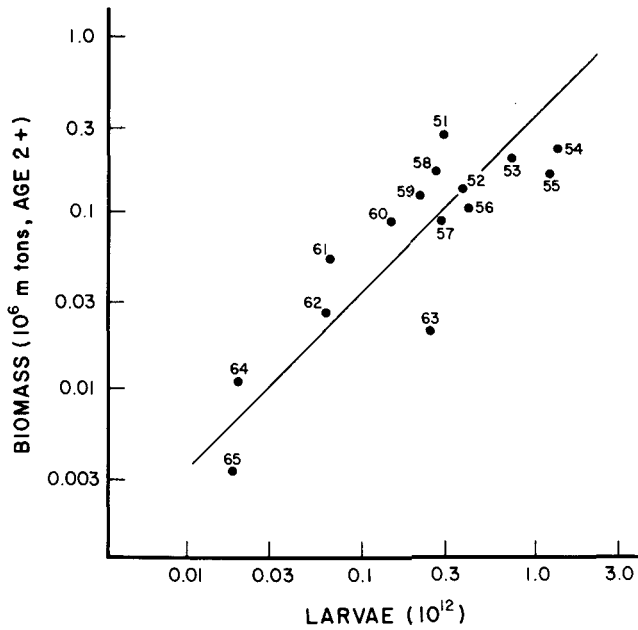where B is sardine spawning biomass (million tons) from

Figure 5. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census, plotted on logarithmic scale.

cohort analysis, and L is CalCOFI larva census (10^9 larvae). The revised relationship (calculated as the mean of the ratios) is

$$B = 0.418 \, L \qquad (s = 0.251)$$

or about double the previous estimate but with much less precision than was formerly attributed to the relationship. Because Smith's (1972) method of calibrating CalCOFI anchovy larva censuses only makes the assumption that anchovies are twice as fecund as sardines, without specifying either actual fecundity, his anchovy biomass estimates are unaffected by this change in sardine biomass calibration.

While showing a large amount of scatter, the CalCOFI sardine larva census estimates agree with the recalculated spawning biomass estimates as much as can reasonably be expected. In this case the cohort analysis was done in ignorance of the larva census values, and the relationship can be used as a validation of results.

Stock-Recruitment Relationship

At low biomass, sardines appear to be fully mature at age 2, but at large biomasses only some of the 2-year-olds are mature. For purposes of this discussion, spawning biomass will be calculated as all fish of age 2 or older, and any lost spawning potential at large biomasses will be subsumed in density-dependent characteristics of the stock-recruitment relationship. Recruitment can be compared with spawning biomass by using Murphy's concept of "potential spawning biomass," being the expected

spawning biomass of a year-class integrated over its lifetime, given particular mortality and growth rates. Murphy's calculation of potential spawning biomass will be modified here: all fish age 2 or older contribute, and the measure of initial year-class strength will be numbers of individuals at age 2 rather than biomass at age 2. The reason for the latter change is that calculation of biomass is dependent upon estimation of the mean weight of an individual in the year class. This, in turn, is strongly affected by the time of year in which most of the 2-year-olds are caught and is, therefore, subject to large and non-relevant sources of variation. Moreover, large fish at age 2 do not necessarily maintain a proportional weight advantage throughout the remainder of their lives. Weights at age are taken from Murphy's Table 16 and will be constant for all levels of biomass. Probable higher growth rates or condition factors when population size is low (MacGregor 1959) are ignored here but could result in as much as a 15% increase in spawning potential.

Previous analyses of the sardine stock-recruitment relationship (Clark and Marr 1955; Radovich 1962; Murphy 1966, 1967) showed density dependence, often by assuming a parabolic or Ricker functional relationship. There is sufficient scatter in the data to fit nearly any type of stock-recruitment function, with no way of determining the true relationship. Other information, such as the geographic composition of the stock (Radovich 1962), can be added to produce a plausible description of the stages in the historical collapse of the fishery. On the other hand, Cushing (1971) concluded that clupeoid stocks tend not to have strong density-dependent regulatory mechanisms, resulting in extreme natural variability and susceptibility to overfishing.

The Pacific sardine has experienced a thousand-fold decrease in abundance since 1932, which makes it necessary to condense the stock-recruitment observations by use of log transformations (Figure 6). Diagonals representing replacement under different fishing mortality rates are plotted for reference. Contrary to previous analyses of the stock-recruitment relationship, this plot shows no functional density-dependent trends whatsoever and agrees with the position of Cushing (1971). There is no increase in recruitment strength relative to parental biomass at low stock sizes, and at every stock size before 1960, recruitments are evenly distributed about the replacement line if there is no fishing mortality. As fishing mortality rate increases, fewer spawnings exceed replacement strength, indicating very little resilience of the population to fishing pressure. For the years 1932 to 1959, the mean replacement success, as measured by $\ln R - \ln P$, is only 0.11, or 12% above replacement at no fishing mortality (the arithmetic mean would be slightly larger). Since year-classes persist for several years and strong year-classes are arithmetically stronger than their loga-
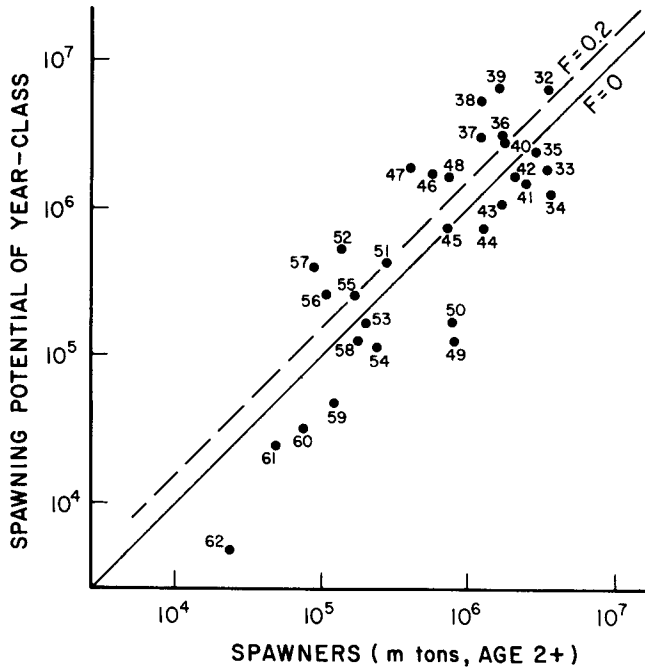
Figure 6. Stock-recruitment relationship of sardine plotted on logarithmic scale.

Figure 7. Sardine population simulation results for various rates of constant fishing mortality rates.

rithmic values suggest, the reproductive potential may be somewhat higher than the above analysis would conclude. Also, successful reproduction seems to occur in sequences of several years' duration, followed by similar runs of poor reproduction. The duration and timing of these runs has a large effect on potential population growth over long periods of time. These factors will be evaluated by simulation in the next section.

The string of poor recruitments since 1958 is remarkable in its duration and magnitude. The most likely explanation is that the high fishing pressure of the 1950's decimated the northern stock to the point where immigration from the southern stock was making up a large portion of the commercial catch. Consequently, estimates of the size of the northern stock are inflated for purposes of estimating its spawning potential (although they may be fairly realistic as a measure of biomass available to the fishery). Presumably, fish of southern origin are less likely to spawn in the cool waters off California. The record since 1958 is not necessarily a series of spawning failures but may be a series of overestimated spawning biomasses for the northern stock.

Population Simulations

Simulation models of the Pacific sardine stock have been used to answer questions relating to management strategies (Lenarz 1971) and to probable futures of the population (Murphy 1967). These simulations employed the Ricker stock-recruitment relationship given by

Murphy (1966) and reflect the production characteristics of that curve. If the functional stock-recruitment relationship is virtually linear, as is suggested in this paper, the previous simulations are unrealistic and contain a tendency toward an equilibrium which may not, in fact, exist.

The effects of two simple management strategies, constant fishing mortality rate and constant quota, will be examined as they would have affected the actual population from 1932 to 1959, the last potentially peak year of population size. The simulation model recreates annual population age compositions based on spawning rates and natural mortality rates as they historically occurred. Fishing mortality rates (determined by management strategy) are the only source of variation in the model: all other elements are fixed. Observed spawning rates, measured as recruits at age 2 per parental biomass age 2 and older, are employed directly. This method of simulating recruitment makes few assumptions as to the true nature of the stock-recruitment relationship. If any density-dependent compensation actually occurs in this relationship, those simulated will tend to be "optimistic" when the simulated population is larger than the actual population from which the spawning rates were obtained. The simulation begins with the age distribution in 1932 given by Murphy (1966, Table 14) and uses the constant weights at age given in his Table 16. Fish of age

3 and greater are treated as fully recruited to the fishery, and age-2 fish are 50% recruited, suffering one-half the instantaneous fishing mortality rate applying to older fish. A natural mortality rate of $M = 0.4$ is assumed for all ages.

The first simulation (Figure 7) examines population trends under three levels of constant fishing pressure: $F = 0.1$, 0.25, and 0.4 The first value allows slow growth, with the population jumping to unreasonably high biomasses in 1958 and 1959 due to the high spawning rates of 1956 and 1957. The second value of $F = 0.25$ causes the population to decline slowly from its peak in the early 1930's, maintaining biomasses between one and two million tons. The third value causes the population to decline to very low levels of about one-half million tons, which must be considered suboptimal. The biomass fell to even lower levels under the actual fishery, giving the simulations an upward bias except for the first few years when the fishing pressure was light and the actual population was larger than the simulation. Thus it appears that $F = 0.25$ is about the maximum constant-fishing pressure that the sardine fishery could have sustained.

An interesting but unrealistic simulation is that of $F = 0$, simulating the growth rate resulting from observed recruitment rates unhindered by fishing or environmental limitation. If the stock-recruitment relationship actually has little or no density-dependent compensation (except at very large population sizes), this growth rate is an approximation of the intrinsic rate of increase (r) in the natural environment. The slope of the logarithm of these simulated population sizes versus time gives an r of 0.082 (8.5%/year). This is considerably less than Murphy's (1967) value of $r = 0.338$, which was based on an extrapolation of his assumed, highly density-dependent Ricker stock recruitment curve to a theoretical zero biomass.

The second simulation holds the annual catch of the fishery constant, approximating a constant-quota system (Figure 8). The simulated population is able to maintain its biomass under a quota of 300,000 metric tons annually but is unable to maintain a quota of 350,000 tons. Due to the "optimistic" bias of the simulation, a safer estimate of maximum sustained yield (MSY) would be 250,000 tons annually. Murphy's (1966) estimate of MSY was 427,000 metric tons (471,000 short tons), which does not seem to have actually been sustainable. The extreme sensitivity of a naturally fluctuating resource to small changes in quota levels indicates the danger of basing management on such an inflexible system. A programmed reduction or cessation of fishing at low biomasses is necessary to provide protection from collapse of an easily overfished resource.
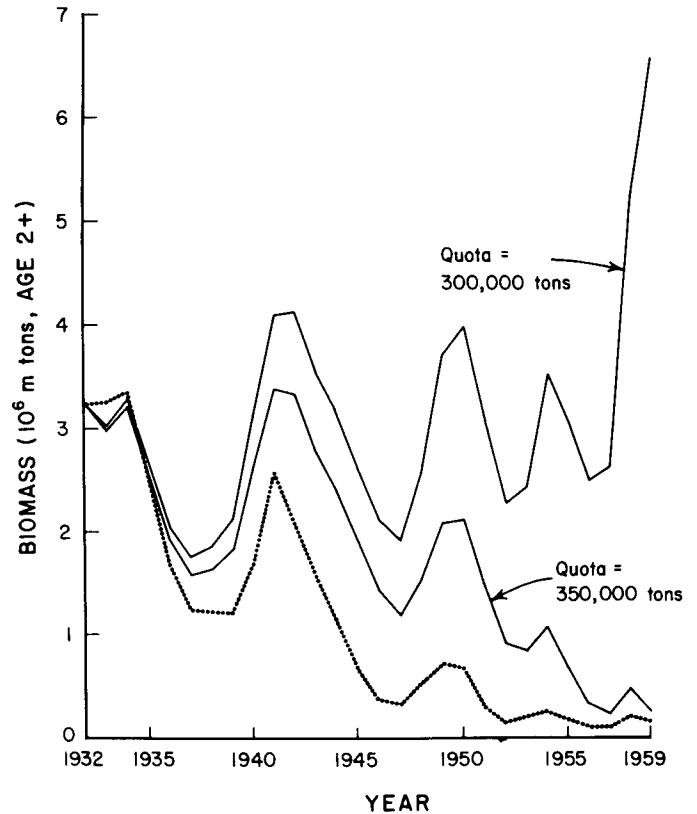
Figure 8. Sardine population simulation results for two levels of annual catch quotas.

This estimate of maximum sustainable yield from the sardine fishery is much smaller than the Gulland potential-yield estimate (Gulland 1970) would give. Using a natural mortality rate of $M = 0.4$ and using the 1932 biomass of 3.2 million metric tons as an estimate of virgin fishable biomass (B_0), potential yield (C_{max}) is estimated to be $0.5 \times 0.4 \times 3.2$ million tons, or 640,000 tons. This is two and one-half times larger than the simulation result and clearly would not be sustainable. The Gulland potential yield estimator appears to require further modification in the case of a naturally fluctuating stock, which may have little density-dependent regulation of recruitment. Two modifications may be suggested: either use as B_0 the smallest population size that has been observed in the virgin state, or use one-half of the Gulland potential yield as a more realistic estimate. For example, the Gulland potential yield from the northern anchovy (Engraulis mordax) central stock has been estimated as one to two million tons (MacCall et al. 1976). One-half of this estimate is 500,000 to 1,000,000 tons, which is much closer to estimates of surplus production based on observed growth rates of the population (Radovich and MacCall, this volume), which project an anchovy MSY of approximately 450,000 tons.

CONCLUSIONS

1. A new time series of biomass estimates for Pacific sardine extending to 1963 is presented, based on a cohort analysis of catches from the geographical area associated with the northern stock. The new population estimates are considerably smaller than those previously published and are, moreover, in better agreement with trends in independent indices of abundance (catch per unit effort, night-light surveys) for California waters.

2. It is not necessary to assume an increase in rate of natural mortality from $M = 0.4$ to $M = 0.8$ in the 1950's to obtain reasonable biomass estimates.

3. A decrease in the relative abundance of 2- and 3-year-old fish occurred in the 1950's, possibly reflecting a progressively southerly origin of year classes. Failure to recognize this change caused a downward bias in previously published estimates of fishing mortality rates for the 1950's, wherein 3-year-old fish were assumed to be fully recruited.

4. The ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one-quarter to quadruple the estimated biomass. The relationship displays the expected statistical qualities, whereas the previously published relationship was artificially precise.

5. A purely functional description of the stock-recruitment relationship since 1932 shows no curvature (density-dependent regulation of recruitment), indicating little resilience to fishing. Had there been no fishing, the stock would, on the average, have done little better than replace itself. The average potential growth rate appears to have been 8.5%/year, with large fluctuations.

6. The apparently poor rates of recruitment in the 1960's are likely to be the result of including immigrant fish from the southern genetic group in estimates of spawning biomass of the northern stock. These southern fish may not be adapted to spawning in the relatively cool waters off California. Recruitment rates of the remaining fish from the northern genetic group may have been quite normal.

7. A simulation model of the sardine population containing "optimistic" biases showed the maximum continuous-fishing mortality rate that the sardine population could have sustained to have been $F = 0.25$ (22% annually.

8. The same model showed that the population could have sustained a constant annual quota of 300,000 metric tons but would have been seriously depleted by a 350,000 ton quota. Due to instability induced by a constant harvest from a fluctuating population, and to the "optimistic" bias of the model, maximum sustained yield for the northern stock was probably about 250,000 tons. This estimate is considerably lower than the previous estimate of 427,000 metric tons (Murphy 1966).

9. The Gulland potential yield estimation (Gulland 1970) would have estimated potential maximum sustained yield to be 640,000 metric tons, which would not have been sustainable. The Gulland estimator may have to be revised downward in the case of populations subject to large natural fluctuations in abundance.

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A MANAGEMENT MODEL FOR THE CENTRAL STOCK OF THE NORTHERN ANCHOVY, ENGRAULIS MORDAX

JOHN RADOVICH
California Department of Fish and Game
Sacramento, CA 95814

ALEC D. MACCALL
California Department of Fish and Game
Southwest Fisheries Center
La Jolla, CA 92038

ABSTRACT

The average growth of the northern anchovy central subpopulation between the years 1951 and 1975, as measured by CalCOFI egg and larva surveys, can be empirically described by a logistic growth curve. The asymptotic maximum population size, or spawning biomass, is 4 million short tons, and the intrinsic rate of increase is 0.36. A maximum average growth rate of 360,000 short tons/year occurs at a spawning biomass of 2 million tons. If the population were maintained at 2 million tons by harvesting surplus production, an estimated 450,000 short tons/year could be harvested. The difference between yield and population growth rate is due to the competing risk of death between fishing mortality and natural mortality. This estimate of potential productivity is smaller than previous estimates, but is better founded.

INTRODUCTION

In the absence of a substantial fishery, there has been some difficulty in getting good estimates of potential yield of the anchovy population. For most years, the catch was less than 5% of the biomass (MacCall et al. 1976), certainly too small a fishery to be able to distinguish fishery-caused effects from other variations (including sampling error).

In the early 1950's, Clark and Phillips (1952) indicated that the anchovy fishery resource probably could not withstand a major fishery at that time. By the late 1950's, as a result of CalCOFI investigations, it had become obvious that the anchovy population had grown, and a potential harvest was believed to be possible. In 1964, Chapman (1964), referred to a harvest rate of 25% of the population, which he felt was a very conservative estimate of the potential harvest. Subsequently, the 25% value was frequently stated as a conservative potential catch of the recruited biomass. It had no biological basis and was viewed with skepticism by a number of scientists.

No further progress was made on estimating maximum sustainable yield (MSY) until MacCall et al. (1974, 1976) applied a technique that has come to be known as Gulland's "quick and dirty" potential yield method (Gulland 1970). This method roughly estimates potential yield from a fishery in which most fishery data is lacking and where the catch is an insignificant portion of the biomass. The Gulland Formula is:

$$Y_{pot} = XMB_0$$

where Y_{pot} = potential yield;

M = instantaneous natural mortality rate;

B_0 = mean virgin biomass of fish above length at first capture;

X = a coefficient which is determined by M, K (von Bertalanffy growth rate[1]), and relative size at first capture (l_c).

Biomass estimates from egg-and-larva surveys were used since they appeared to be the most reliable source. These correspond to the spawning biomass which may not differ substantially from the exploitable biomass since the fish appear to be recruited and mature at one year of age (Table 1). However, anchovies become available to the fishery at about the time of first spawning, so spawning biomass as measured by egg and larva surveys must therefore represent initial rather than average spawning biomass for the season. Thus, the biomass estimates used by MacCall et al. were larger than mean biomass, and potential yield was similarly overestimated.

A total mortality of $Z = 1.1$ was calculated from catch curves for five different years (MacCall 1974). F was obtained from a ratio of the catch to total biomass estimates. These averaged 0.03. This indicates that M cannot be smaller than 1.00 or 1.05. They used calculated values of 0.3 for Bertalanffy growth parameter K and 165.5 mm (standard length) for von Bertalanffy parameter L_∞. Since recruitment occurs at over a range of 85 to 115 mm, 105 mm was used as the estimate of l_c. Considering the stock very near virgin state, Gulland's equation $Y_{pot} = XMB_0$ was used to estimate potential yield using an M of 1.05 and K of 0.3, an l_c of 105.0 mm, and an L_∞ of 165.5 mm,

$$\frac{M}{K} = \frac{1.05}{0.3} = 3.5 \text{ and } c = \frac{l_c}{L_\infty} = \frac{105.0}{165.5} = 0.63.$$

Using the values for M/K and c, the value of the coefficient X would be about 0.6, from Gulland's table (Gulland 1970, p. 3). The maximum potential yield should therefore be about 60% of the mean fishable biomass. From this, the potential yields from 1951 through

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[1] The von Bertalanffy growth curve is $l_t = L_\infty(1 - e^{-K(t-t_0)})$ where l_t is length at time t, L_∞ is asymptotic maximum length, K is a growth constant and t_0 is hypothetical age at zero length.

TABLE 1

Anchovy Biomass Estimates for the Central Subpopulation, and Annual Catches (Thousand Short Tons).

Year	Biomass*	Catch			
		U.S.			
		Commercial	Live Bait	Mexico	Total
1951	180	3	5	.....	8
1952	156	28	7	.....	35
1953	510	43	6	.....	49
1954	768	21	7	.....	28
1955	846	22	6	.....	28
1956	485	28	6	.....	34
1957	1,172	20	4	.....	24
1958	1,479	6	4	.....	10
1959	1,514	4	5	.....	9
1960	1,540	2	5	.....	7
1961	1,159	4	6	....	10
1962	2,986	1	6	1	8
1963	4,254	2	4	1	7
1964	2,900	2	5	5	12
1965	4,659	3	6	10	19
1966	3,572	31	7	15	53
1967		35	5	22	62
1968		15	7	16	38
1969	2,999	68	5	4	77
1970		96	6	31	133
1971		45	6	22	73
1972	2,784	69	6	36	111
1973		133	6	16	155
1974		83	6	44	133
1975	3,603	159	6	61	225

*Biomass estimates supplied by Paul Smith (NMFS). These estimates are in the process of being revised and are preliminary.

TABLE 2

Biomass and Corresponding Potential Yields for the Total Population and the Central Stock for 1) the 20-year Period of Observation and 2) after the Depletion of Pacific Sardine Stock.*

Time period	Population	Biomass mean and range (10^3 tons)	Corresponding potential yields (10^3 tons)
1951-69	Total	3,200 (640-7,800)	1,900 (400-4,700)
1951-1972 after After sardine collapse	Central stock	2,600 (290-6,200)	1,500 (200-3,700)
1965-69	Total	4,600 (2,200-7,800)	2,800 (1,300-4,700)
1965-72	Central stock	4,000 (2,050-6,200)	2,400 (1,200-3,700)

*After MacCall et al. (1976).

1972 were calculated (Table 2). These averaged from 1.5 to 2.4 million tons for the central subpopulation, although a very wide range was given. MacCall et al. concluded that the central stock of northern anchovy can produce a yield from 10 to 20 times higher than present catches. In view of the numerous collapses of clupeid fisheries and the known low abundances of anchovies in the recent past, their statement appeared extreme. While such levels of harvest might well be feasible for a short

while, their sustainability appeared questionable.

The anchovy fishery is being subjected to strong pressure for expansion. The Mexican fleet is unilaterally developing their anchovy reduction industry. Passage of the Fisheries Management and Conservation Act of 1976 by the U.S. Legislature portends a likely increased harvest, if not by U.S. fishermen, then possibly by foreign fleets under the provisions of the Act. A more reliable estimate of sustainable yield of anchovy is needed. This estimate would preferably be based on observed dynamics of the northern anchovy central stock rather than on broad generalizations based on characteristics of different species in different environments, as is the Gulland method.

In 1975 we noticed that since 1950 the anchovy population seemed to have at first grown slowly, then accelerated rapidly, and finally leveled off somewhere around 4 million tons. This pattern was very similar to the logistic growth curve. The low abundance of anchovy in 1951 has not been attributed to any demonstrable cause. The species was not harvested to any extent, ruling out overexploitation. The hypothesis of interspecific competition from the Pacific sardine (Sardinops sagax caerulea) has been invoked (Murphy 1966), seemingly verified (Silliman 1969), and set back (Soutar and Isaacs 1974). Smith (1972) showed the anchovy population to have been relatively large (between 2 and 3 million tons) in 1940 and 1941. Such a population size at a time when sardines were also abundant is utterly inconsistent with the competition hypothesis. It appears much more likely that the anchovy suffered a sequence of recruitment failures probably near the end of the 1940's. Two other local pelagic species, the Pacific sardine (MacCall 1979) and the Pacific mackerel, Scomber japonicus (Parrish 1974; Parrish and MacCall 1978), showed severe reproductive failures in the period 1949-1951. A third species, the Pacific bonito (Collins and MacCall 1977), became very scarce in California waters during the early 1950's. The anchovy may well have suffered similar reproductive difficulties.

Following this decline, after 1951, the central stock first increased its density at the center of its distribution in southern California waters. Then, with the warm ocean temperatures of the late 1950's, the central stock extended its range to the waters of central California, which had originally been inhabited by an apparently local population. Since 1960 the density of fish in the occupied areas increased, reaching relative stability in the late 1960's and early 1970's.

If the low abundance in 1951 was due to some limiting factor, expansion of the central stock can be interpreted as an increase in carrying capacity relative to that prevailing in the early 1950's. If the low abundance was due to a long series of poor year-classes because of environmental variability and the anchovy subsequently

experienced a long series of favorable reproductive conditions, the present level of abundance could be very temporary, with no level of fishing necessarily being sustainable. Until the actual cause of the increase is determined, the possibility of a "natural" decline to a lower population must be be considered in any management strategy. However, growth rates of the population during that favorable period provide a basis for estimating reasonable interim harvest rates, and the interim period may continue for an indefinite period of time. The sedimentary scale records of Soutar and Isaacs (1974) indicate that low anchovy populations are a rare event.

METHODS

A logistic growth curve is based on the assumption that at very low population sizes the population growth rate is limited by the small biomass present, while at large population sizes the growth rate is reduced because all suitable habitat, food, or other resource necessary for existence is utilized, allowing no further expansion. Specific population growth rate (dB/Bdt) decreases linearly with the fraction of the maximum carrying capacity that is utilized. Maximum growth rate occurs at a population size that is exactly halfway between zero and the maximum capacity.

Various fisheries models, termed "production models," utilize this concept, wherein the fishery controls the population size so as to hold it at a level optimal for fish production. If the yield from the fishery matches the potential increase, an equilibrium is reached. The highest equilibrium point is called maximum equilibrium yield or maximum sustainable yield (MSY). A drawback with such fisheries models is that they must use a proxy (or substitute) for the population estimate by assuming a relationship between effort or catch per effort and the actual population. This may introduce serious biases as each of the authors of this paper have suggested previously (Radovich 1973, 1975, 1976; MacCall 1976). However, with the anchovy, we are in a unique situation of having fishery-independent estimates of population size of the stock during a 25-year period of considerable population growth.

If we make the assumption that in 1950 the anchovy stock was very low (for whatever cause or restraining influence) and subsequently grew in logistic fashion to the maximum carrying capacity of the geographical area, due to the removal of the initial restraining influence, we can obtain essentially the same management information that usually is attempted to be derived from a fishery by the use of production models.

The CalCOFI spawning biomass estimates for the central subpopulation of northern anchovy (Table 1, Figure 1) are assumed to represent the biomass in the spring of each year, which is the time of peak spawning activity.

These data were used to estimate the parameters of the logistic growth equation.

$$B_{(t)} = \frac{B_\infty}{1 + e^{-r(t-t_O)}}$$

where: $B_{(t)}$ is the biomass at time t,

r is the intrinsic rate of increase,

B_∞ is the asymptotic maximum biomass, or carrying capacity, and

t_O is the time of inflection of the growth curve (time at which $B_{(t)} = \frac{1}{2} B_\infty$).

The biomass data were first transformed by taking logarithms to obtain a constant error variance. They were then submitted to a curvilinear least squares regression algorithm (Conway et al. 1970), which employed the corresponding log transform of the above logistic equation. Due to log transformation, parameter B_∞ was estimated as a geometric mean, so the correction of Beauchamp and Olson (1973) was applied to obtain the proper arithmetic mean. The resulting parameter estimates were

$B_\infty = 4.0$ million tons,

$r = 0.36$,

$t_O = 1959.6$,
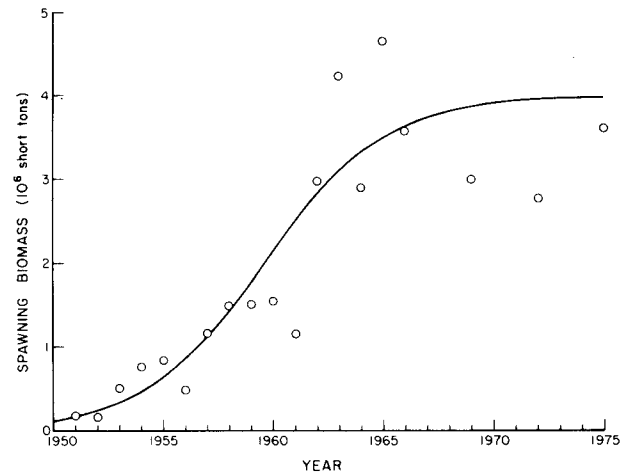
and the curve is plotted in Figure 1.

Figure 1. A logistic growth curve fitted to the spawning population biomass estimates of the central stock of the northern anchovy from 1951 to 1975.

The first time derivative of the logistic growth equation gives population growth rate as a function of biomass:

$$\frac{dB_{(t)}}{dt} = rB \frac{B_\infty - B}{B_\infty}$$

This equation describes growth rate as a domed curve rising from the origin to a peak growth rate at $\frac{1}{2}$ B_{∞} (Figure 2). Since there is considerable variation about the regression line in Figure 1, this estimate of growth rate must be interpreted as an average (itself subject to error of estimation) about which actual observations will vary.
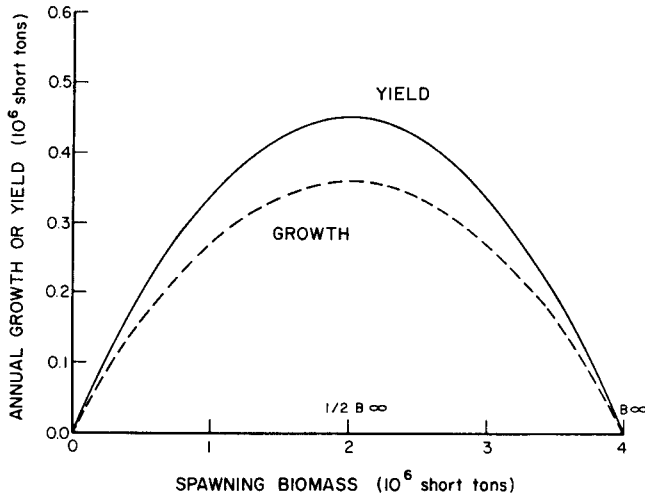

Figure 2. Differential form of the growth curve (dashed line) and yield curve (solid line) of the northern anchovy.

If a harvest is taken each year such that all the expected growth is caught immediately before the biomass is measured, the biomass would tend to remain unchanged from measurement to measurement, and equilibrium yield would be obtained. In this manner, the growth rate curve can be interpreted as an equilibrium yield curve. However, if the catch were made just after measurement of biomass, somewhat more fish could be harvested while maintaining equilibrium, since many are likely to die of natural causes before the next biomass measurement. For an anchovy fishery acting continuously throughout the year, equilibrium yield would be greater than the corresponding growth potential by perhaps 25%. The actual percentage would vary with natural mortality rate and with the seasonality of the fishery. Thus, for the northern anchovy central stock, we estimate the peak growth rate would be 360,000 tons/year at a spawning biomass of 2.0 million tons, whereas the equilibrium yield at the same biomass would be closer to 450,000 tons/year (Figure 2), which is our estimate of maximum sustainable yield.

DISCUSSION

This use of the logistic growth model violates several assumptions that normally underlie the logistic equation. However, many of these assumptions are simply dispensed with by treating the logistic as an empirical de-

scription of the population growth curve. We need not be concerned with the mechanisms by which logistic growth is usually assumed to occur.

Nontheless some assumptions can bear serious discussion. By using the logistic curve as a regression line, about which observations vary, the original deterministic nature of the curve is lost. Therefore, the growth rate curve and derived production curve now represent average responses, about which we expect variation from year to year. This implies that equilibrium biomass may not be well-defined under any particular fishing strategy, and many years of observations may be necessary to determine the true population response to fishing pressure.

The model also assumes that no fishing occurred during the period from which the data came. A moderate fishery existed for a few years in the early 1950's and again since the mid-1960's. Since the population was low in the early 1950's, the earlier fishery probably contributed to a downward bias in our estimate of the intrinsic rate of increase, whereas the later fishery caused a downward bias of perhaps 0.05 million tons (the magnitude of the fishery) in B_{∞}. Finally, if the increase in carrying capacity were not immediate in 1951, but increased in stepwise fashion, the estimate of r is likely to be low. This increase in carrying capacity may have occurred by expanding the geographic range of the stock. On the other hand, if the geographic range of the stock shrinks under exploitation (which has been observed in other fisheries), the production curve may be realistic.

At large biomasses, considerable amounts of fish in excess of MSY can be harvested, but these harvests are temporary and will only serve to bring the biomass down to a level where theoretical maximum sustained production would occur. Various harvest strategies can be drawn in the diagram (Figure 3). The line rising from the center to the upper right on the management diagram represents the harvest that will bring the population to optimum size[2] in the very next year. This line, combined with the production curve, divides the diagram into four sectors. In Sector I the population will usually increase, and it will be above the optimal the following year. If a harvest enters Sector III, the population will usually increase, but it will not usually reach the optimum size the following year. At large population sizes, harvests in Sector II will take advantage of the biomass in excess of that needed for maximum growth. In Sector IV the population is being overfished; it will usually be declining and will be less than optimum the following year.

A steep harvest line will allow maximum utilization of excess biomass but would result in large year-to-year changes in catch, which could create problems with the economics of the fishing industry. A more horizontal

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[2] "Optimum" as used here refers to that population size producing maximum yield and does not imply any other kind of optimality.

harvest line would tend to stabilize annual fluctuations. In drawing in such a harvest line, some errors will be compensated, and optimal harvest will be likely. For example,
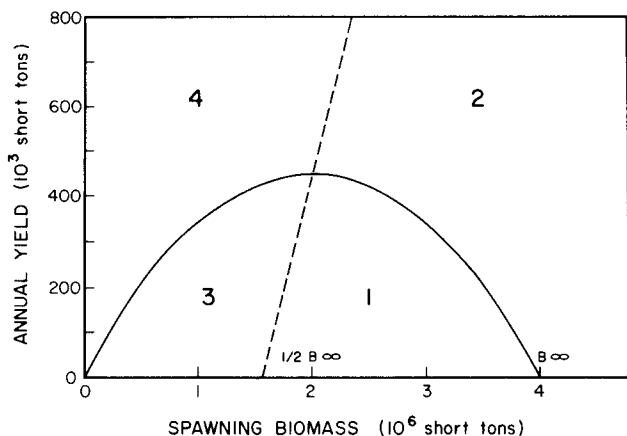

Figure 3. The yield curve divided into four sectors by a line representing the locus of catches that would result in an optimum size population at the beginning of the following season.

consider a harvest line which is a diagonal straght line passing from 0 harvest at ½ optimum biomass through MSY at optimum biomass and extending upward with larger biomasses (Figure 4). If the true harvestable production of the population is larger than we have shown, then such a harvest line would result in the fishery coming into an equilibrium at a highler level of catch but also at a higher biomass. Thus, the danger of overfishing the population is small, since large harvests would be allowed only when the population is very large; if the population can sustain such largest harvests, it will do so without danger of seriously depleting the stock. If biomass itself contributes to the objectives of management, it may be appropriate to shift the intersection of the harvest policy toward maintenance of larger biomass at a small reduction in yield. For example, the second alternative policy in Figure 4 would result in a gain of 320,000 tons of biomass while only 12,000 tons of yield would be lost relative to the first alternative policy.

An important feature of this harvesting strategy is the limit of biomass below which no harvest is allowed. This is a virtual guarantee that the resource cannot be depleted by overfishing. It also allows a maximal rate of recovery in the event of a natural decline in biomass as is assumed to have happened in the late 1940's. Finally, it recognizes the importance of the anchovy as a major trophic link in the food web. Although there is undoubtedly room for harvest of anchovies from the ecosystem, it would be unwise to place the importance of that harvest above the maintenance of the ecosystem that produced it (as well as
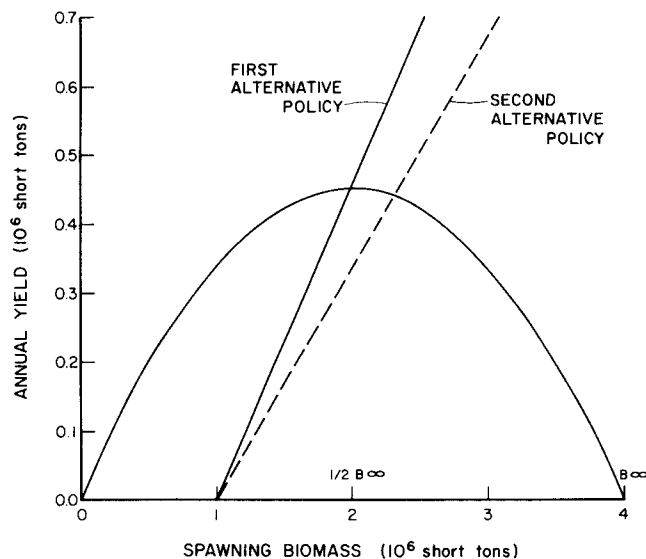
Figure 4. Alternate fishing strategies. The dshed line represents a policy that would allow for an average biomass 320,000 tons larger than that represented by the solid line, with an average loss in yield of 12,000 tons.

a wealth of higher predators).

The problem of the effects of the fishery on bait and recreational species has not been resolved; however, it is interesting to note that the heaviest runs of subtropical sportfish in northern California occurred in the mid-to-late 1950's (Radovich 1961). This took place when the biomass of anchovies was growing the most rapidly. It therefore appears that, under favorable environmental conditions, forage at the optimum population size, $B_\infty/2$, was adequate to support an immigration of voracious game fish, as well as forage for the resident demersal fishes in southern California and for the live bait requirements of the recreational fishing fleet. It is important to note that under unfavorable environmental conditions, catches of migratory predator fish may be poor despite an abundance of anchovies. Many factors appear to influence migrations and abundance of predators, and much remains to be learned about their interactions. In addition, there does not appear to have been any known increase of other predators on anchovies, such as birds, since the anchovy biomass increased from its mid-1950's level.

When we compare this estimate of productivity with those made by the Gulland potential yield method, the Gulland estimates appear to be high. A similar discrepancy was shown by MacCall (1979) for the Pacific sardine fishery, on the basis of simulations. Besides the previously discussed error of confusing egg and larva biomass estimates with mean biomass, use of the Gulland method appears to assume an underlying stability of the resource that may not hold. In any case, our estimate of productivity, like the Gulland potential yield estimate, is not based on actual fishing experience and is meant to be modified as further information is gained.

SUMMARY

In summary then, this method of estimating anchovy productivity has a number of advantages over other methods:

1. It is based on observed growth rates instead of assumed rates.

2. It does not rely on fishery catch and effort data and thereby avoids the serious biases encountered in the use and interpretation of effort measurements.

3. It gives a far more cautious estimate of MSY (about 450,000 tons), which seems more consistent with other studies, than Gulland's "quick and dirty" methods.

4. Management strategy should be directed toward maintaining an optimum spawning biomass, which may result in a more variable fishery than MSY obtained by other methods, but would not run as large a risk of collapse.

The minimum of the logistic curve (Figure 1) at zero and the carrying capacity at 4 million tons can be fit easily, but the slope at the point of inflection isn't quite as clear. This means that the maximum equilibrium catch may be somewhat higher or lower depending on a few points which may vary quite a bit; however, the optimum population size still appears to be about one-half the carrying capacity, and the management strategy of attempting to keep the population at its optimum size is valid. One may simply proceed with caution and watch where the population tends to stabilize, before making further adjustments.

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LARGE-SCALE BIOLOGICAL EVENTS IN THE CALIFORNIA CURRENT

PATRICIO A. BERNAL
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, CA 92093

INTRODUCTION

In addition to the seasonal signal, which can be statistically resolved for both physical and biological variables, the California Current system undergoes large-scale non-periodical fluctuations. Based on the record of varved sediments of biological origin preserved in anaerobic basins, these fluctuations seem to have been the rule rather than the exception in the past (Soutar 1967, 1971; Soutar and Isaacs 1969, 1974). For example, the combined biomass of the Pacific sardine, *Sardinops caerulea,* the northern anchovy, *Engraulis mordax,* the Pacific hake, *Merluccius productus,* and the Pacific saury, *Colalabis saira,* have experienced fluctuations of at least one order of magnitude during the last 150 years (Soutar and Isaacs 1974). Thecosomatous pteropods and heteropod molluscs, members of the planktonic assemblage of the California Current, also showed large departures from their long-term density in the sediments, with maxima up to four times the mean (A. Soutar, personal communication).

Since 1949 the CalCOFI project has been collecting zooplankton samples on which zooplankton displacement volumes are routinely determined. These volumes represent a readily available estimate of the biomass of zooplankton, and with some caution they can be interpreted as an index of the secondary production of the epipelagic ecosystem in the region. Smith (1971) presented detailed monthly charts of displacement volumes for the period 1951 through 1966, discussing in detail the methods and major trends present in the record.

In an effort to identify periods of unusually high or low secondary production in the epipelagic ecosystem, this report reexamines the CalCOFI record of zooplankton displacement volumes for the 21-year period extending from 1949 through 1969, using the techniques of time-series analysis.

MATERIALS AND METHODS

A good summary of the methods and techniques used in field and laboratory to obtain the zooplankton displacement volumes is given in Kramer et al. (1972), and they will not be repeated here.

The five geographical areas of the California Current chosen for this study are shown in Figure 1. In delimiting them, consideration was given to the hydrographic (Reid et al. 1958) and faunistic (Brinton 1962; Alvariño

1964; Fleminger 1967; McGowan 1968) patterns present in the region. Although this is a region of confluence for different faunas, these areas represent a partition of the CalCOFI sampling grid with some faunistic meaning. Area I in the north should be dominated by subarctic and transitional forms. Areas III (in part) and IV present a fauna that becomes increasingly dominated by equatorial forms. Area II, on the other hand, is an area where intense stirring and mixing of different water masses and a parallel mixture of faunas occur; here representatives of the three regimes already mentioned are found interspersed in the samples. Area V, lying close to the outer boundary of the current, is dominated by species that belong to the assemblage of the Subtropical Central Pacific Water mass.

Time series of zooplankton biomass for each area were derived, with each element of the series-vector being the average over space of the stations within that area occupied on a given month. This procedure filters out the short-term (daily) and the small-scale spatial (patchiness) variability. The time series were standardized to give a mean of zero and unit standard deviation, and then they were codified into integer values with one unit being equivalent to ± 0.2 standard deviation units; hence, a codified value of ± 5.0 is equivalent to one standard deviation. The absolute unit used by CalCOFI to report zooplankton displacement volumes is $ml/1000$ m^3; the necessary information to convert codified values back to absolute units is given in the Appendix, which follows this report.

Because the station-to-station data and the averaged values for the five areas have frequency distributions that are clearly non-normal, a logarithmic transformation taking the natural logarithm of each sample was applied to the original data base, and areal averages were recomputed. The improvement toward normality that resulted from the transformation was quite apparent when frequency distributions were compared by plotting them on probability paper. It should be noted that in the log-transformed series, the average corresponds to the geometric mean of the original values (Bagenal 1955).

Preliminary work and previously published information (Smith 1971; Kramer and Smith 1972) indicated the presence of a seasonal signal in the record. Because my interest was in long-term fluctuations, a set of seasonally corrected series was computed. The correction consisted of calculating the monthly deviations of the areal
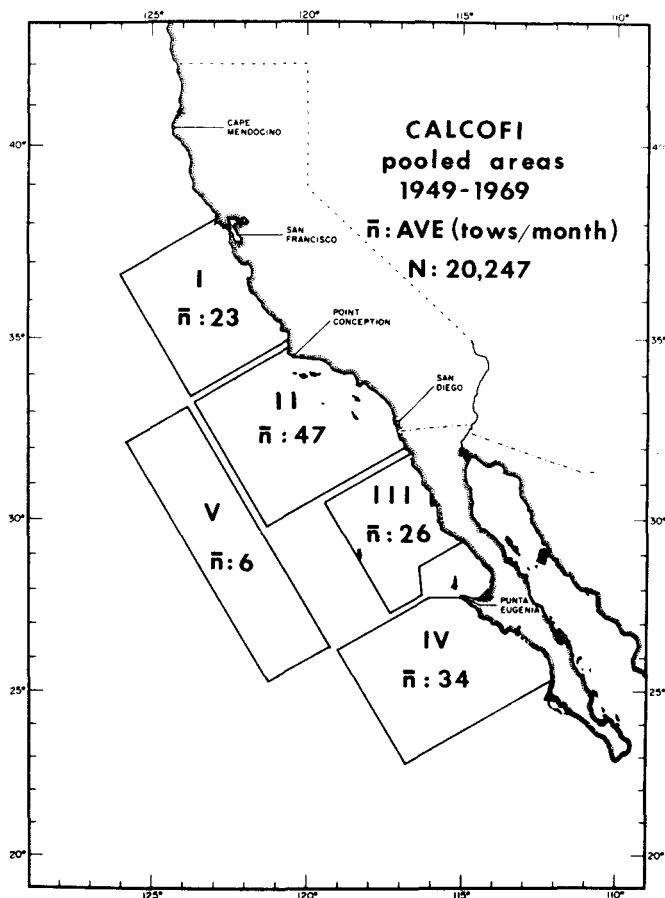
Figure 1. Geographical areas in the California Current over which spatial averages of zooplankton volume were computed: "n" is the average number of samples pooled into a typical monthly estimate; "N" is the total number of plankton tows used in the study.

averages by subtracting the 21-year monthly average and standardizing it with the corresponding 21-year monthly standard deviation. This is equivalent to eliminating the average seasonal cycle term by term.

Autocorrelation functions plus auto- and cross-spectral estimates were computed for the seasonally corrected series for Area I through IV. Area V was excluded because very few observations were available.

The autocorrelation function is the serial correlation of a series with itself, and it provides information of how neighbouring points are correlated. In our case a high autocorrelation value means that a high or low biomass will tend to broadcast its influence in the future of the series, producing more high or low values than expected if no autocorrelation existed. Broadly speaking, it measures the "inertia" of the series.

Spectral analysis performs a decomposition of the total variance of a series into independent—orthogonal—components as a function of frequency or period. The area under the spectral curve is equivalent to the total variance; hence, peaks in the spectral density function signal out frequencies or periods that account for a high proportion of the variance, and the frequency or period at which these peaks occur indicates how the maxima (or minima) are spaced in the time domain. For example if a peak occurs at a frequency of 0.05 cycles/month, this means that maxima (or minima) of biomass tend to occur every 0.05^{-1} months apart, i.e. 20 months.

Spectral analysis also permits the comparison of two or more time series. The coefficient of spectral coherency is the ratio of the cross-spectrum of two series and the geometric mean of both auto-spectra (Robinson 1967). Accordingly, spectral coherence measures the common variance at any given frequency of the two time series being compared. If the series maintain, for any given frequency, a fixed phase relationship, this ratio attains its maximum value of 1: the complete "coherent" case. Conversely, if the phase relationship changes randomly, the ratio becomes zero: the completely "incoherent" case. A high coherency at a given frequency between two time series means that peaks in their spectra coincide at that frequency and that the spacing between maxima (or minima) of biomass is more or less the same.

RESULTS

The five time series of untransformed codified values are presented in Figure 2. The series show some very high peaks of biomass that occur simultaneously for more than two areas. During 1950 there are extreme values in Areas I, II, III, and V; during 1953 there are extreme values in Areas II and III; 1956 shows distinct maxima in all areas except II. On the other hand, the biomass values remained consistently below the long-term mean during most of 1958 and parts of 1957 and 1959.

The log-transformed time series are presented in Figure 3. The major features are essentially preserved and the transformation reveals more clearly the minima in the record, especially during years 1957 through 1959.

The seasonally corrected series in Figure 4 show the long-term variation of biomass in the California Current. It is apparent that underlying the seasonal signal there are long-term trends that occur in more than one area at the same time. In particular, years 1950, 1953, and 1956 present simultaneous maxima in at least two areas; and years 1958 and 1959 show a coherent set of minima in four areas.

Figure 5 shows the autocorrelation functions for the four areas upon which the techniques of spectral analysis were applied. The rate at which the autocorrelation function decays as a function of time lag is inversely proportional to the time constant of the process being analyzed, i.e. a fast decay corresponds to a process with a short time constant and vice versa. From Figure 5 it is clear that the characteristic time scale varies from area to area. Area I, the northernmost area in the region, has a
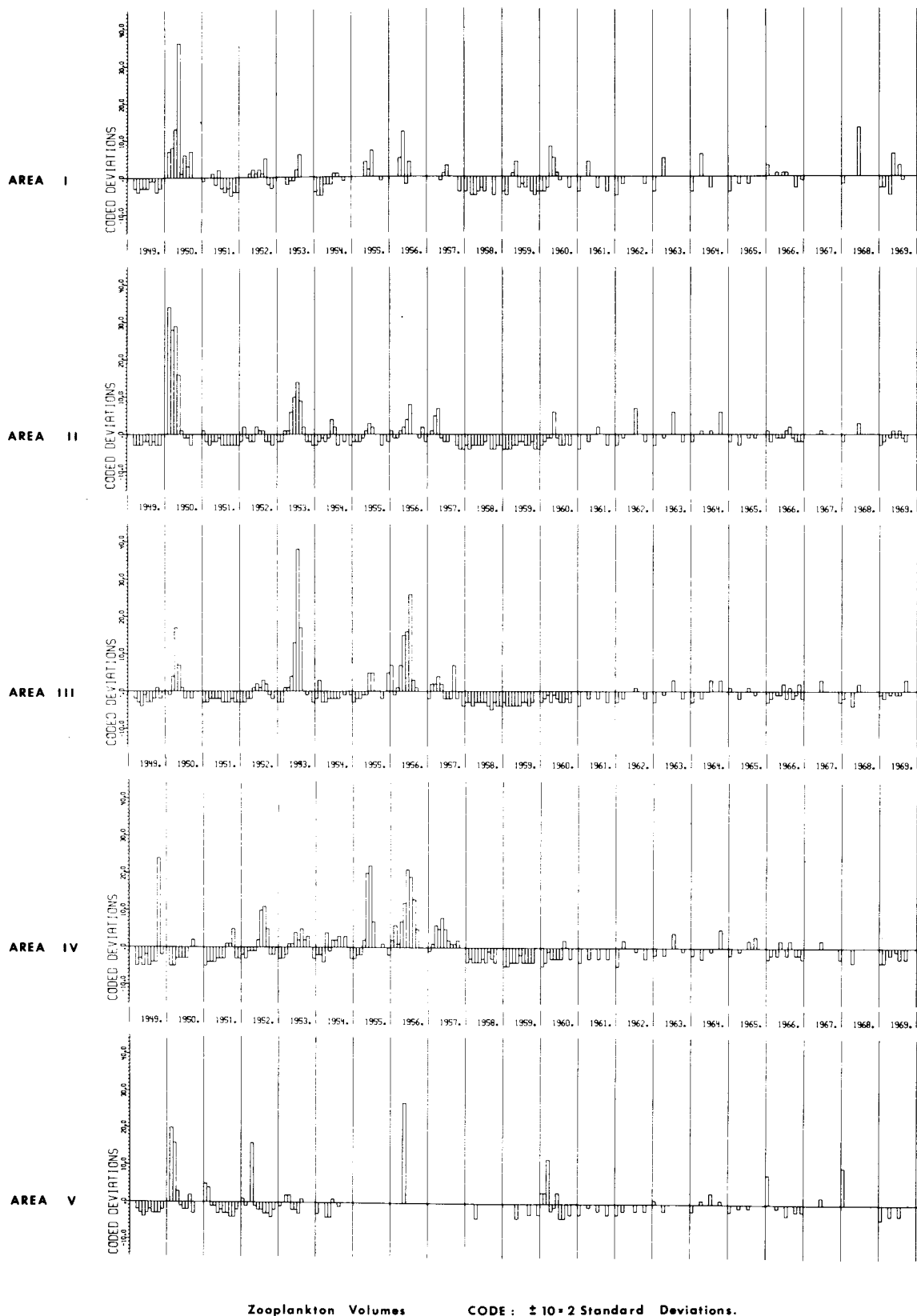
Figure 2. Time series of untransformed monthly averages of zooplankton volume for all five areas. Values plotted are codified deviations from the 21-year mean. Means and standard deviations for all areas are given in the Appendix.

Log$_e$ (Zooplankton Volumes)   CODE : ± 10 = 2 Standard Deviations.

Figure 3. Time series of monthly averages of log$_e$ zooplankton volume for all five areas. Values plotted are codified deviations from 21-year mean. Means and standard deviations of log$_e$ zooplankton volume for all five areas are given in the Appendix.
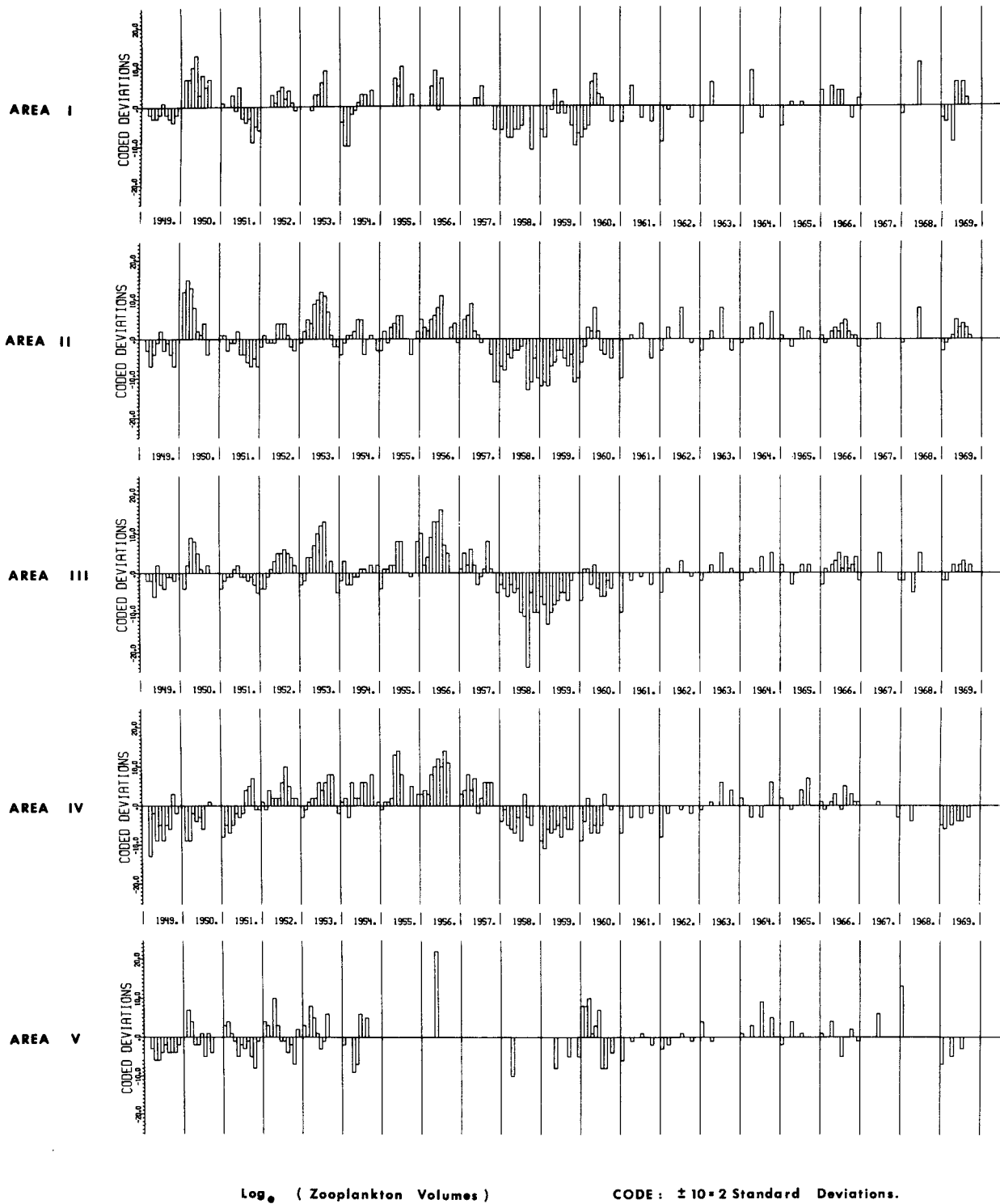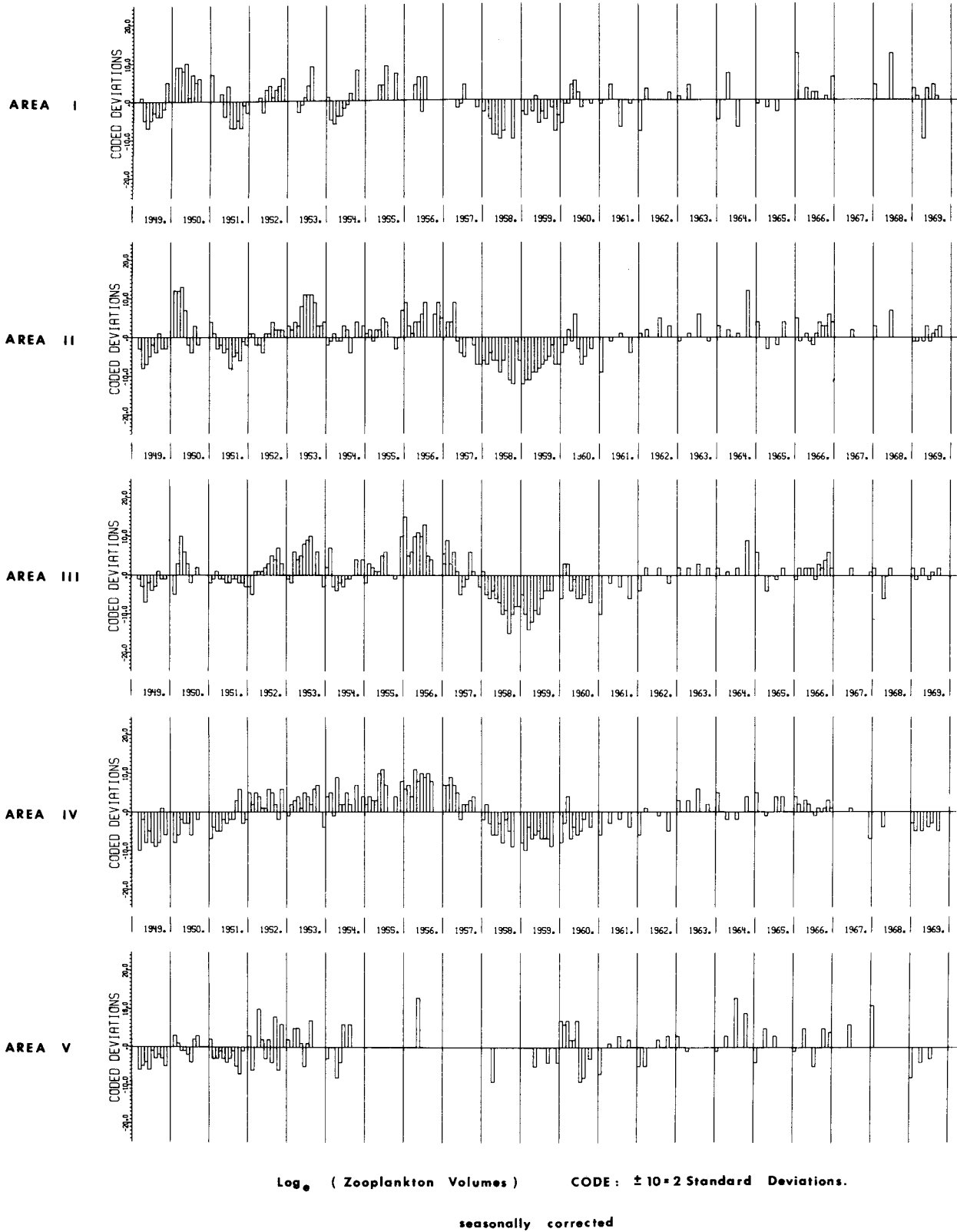
Figure 4. Time series of seasonally corrected monthly averages of log$_e$ zooplankton volume for all five areas. Values plotted are codified deviations from the 21-year monthly averages standardized against 21-year monthly standard deviation. Monthly means and standard deviations are given in the Appendix.
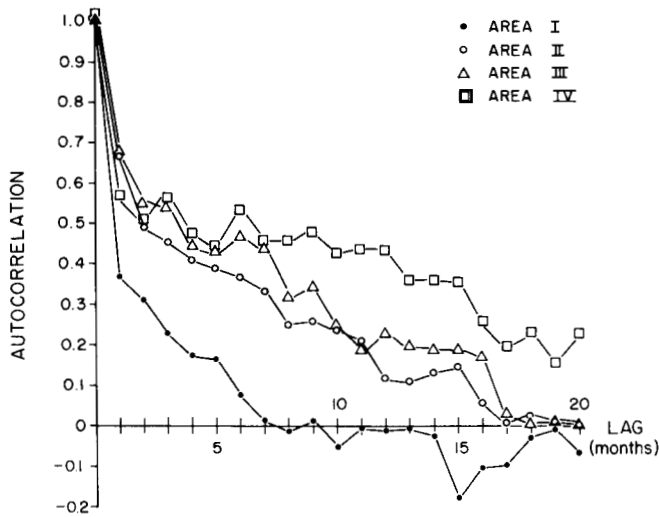
Figure 5. Autocorrelation functions for Areas I through IV: Y-axis in product-moment correlation coefficient units; X-axis in months.

TABLE 1

Percentage of the Total Variance in First Maximum and Selected Bands. Frequency unit: cycles/month

| | First Maximum | | Frequency Bands | | |
	Frequency	% Variance	<.025	0.025-0.050	<0.050
Area I	0.033	4.95	16.75	18.17	34.93
Area II	0.0083	12.59	44.72	11.72	56.43
Area III	0.0083	14.36	46.10	8.18	54.28
Area IV	0.0083	21.44	53.97	3.27	57.24

much shorter time scale, less than 7 months, than the rest. Areas II and III have an intermediate temporal scale of about 17 months, and Area IV has a rather long time scale of about 23 months, a value not shown in the figure.

Area I has consistently higher absolute values of biomass than the other four areas, and its monthly averages form a high peaked function, with its maxima occuring during the month of May. The fact that the dominant time scale of this seasonally corrected series is still of the order of 7 months might be interpreted as an expression of the strong influence of seasonally related effects superimposed on lower frequency components. Because the seasonal correction used is rather insensitive to phase shifts, year-to-year changes of phase ("early" or "late" biomass maxima) might account for this behaviour; furthermore, the effects of phase shifts might be more important here because this time series has the highest root mean square of all. Nevertheless, the possibility that the short time scale might be a spurious result introduced by the frequency of sampling cannot be ruled out.

The series in Figure 4 show a low frequency sine-wave pattern in the southernmost areas, which is most developed in Area IV. The emergence of this pattern is consistent with the north-south trend of increasing temporal scale suggested by the autocorrelation functions.

Figure 6 shows the four auto-spectral plots. The main feature of these plots is that a large fraction of the total variance lies within the low-frequency band, i.e. frequencies less than 0.05 cycles/month or with periods larger than 20 months. Table 1 gives some relevant numerical results from this analysis. The north-south trend of increasing temporal scale of biomass fluctuations that was evident from the autocorrelation functions is

paralleled here by an increasing proportion of the total variance clustered in the low-frequency band. This means that as one moves from north to south an increasing amount of variability is accounted by some slow-response, large-scale process. Another result that points in the same direction is the increasing proportion of the total variance associated with the first maximum in each spectrum, a proportion that increases from 4.95% in Area I to 21.44% in Area IV.

Figure 7 shows the spectral coherency plots for the three area pairs that are contiguous in a north-south direction, with the corresponding 90% confidence limits. Although the coherence ratio fluctuates as a function of frequency, it is clear that the series pairs reach highly significant coherencies in the low-frequency band. This means that the separation in time between maxima and minima of biomass tends to be the same for the different areas.

Based on these results, I have defined five discrete events characterized by the occurrence of very high or low biomass over large extents of the California Current region. They were identified by applying the additional statistical criteria of lying outside the interval bounded by ± 8 codified units (± 1.6 standard deviation units), and by this standard we can accurately call them unusual events. Table 2 summarizes the main features of these events.

DISCUSSION

It is my strong opinion that, because of their magnitude and areal extent, the periods with very high or low biomass represent very important ecological events that cannot be the result of the unforced, free response of the local epipelagic ecosystem. For example, the biomass of copepods, which represent on the average one third of the total macrozooplankton biomass, diminished one order of magnitude (44.85 gm/1000 m³ to 4.15 gm/1000 m³) from October 1955 to October 1958 (Isaacs et al. 1969). This change is equivalent to a power flux of 4×10^{12} watts in the California Current alone (Isaacs 1975). During these unusual periods, changes in horizontal advection, as well as other physical processes associated with an external input of nutrients, must be acting as forcing functions for the epipelagic ecosystem.
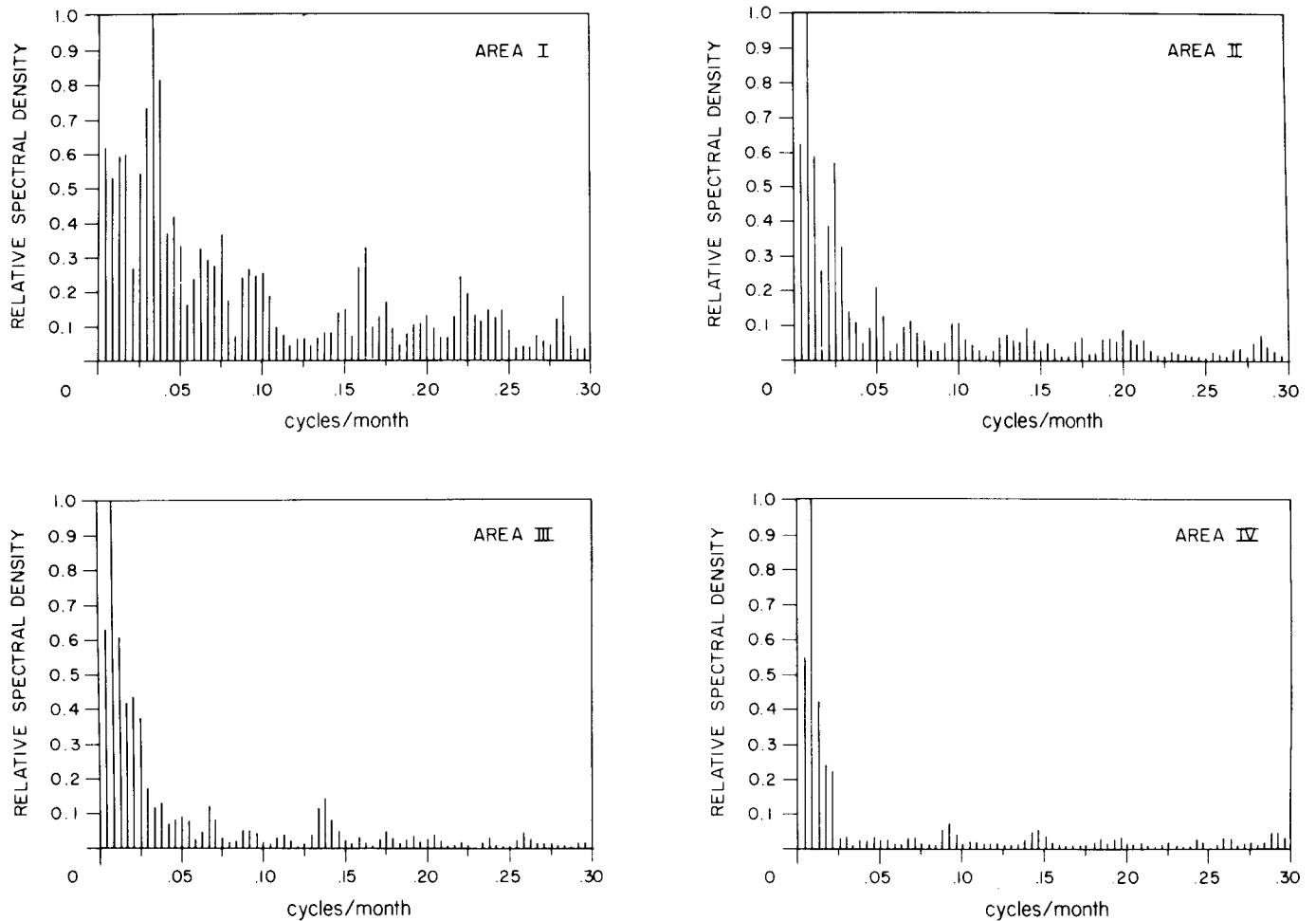
Figure 6. Auto-spectra for Areas I through IV. Y-axis is labeled "Relative Spectral Densities" because all densities were scaled with respect to the largest value: thus, the highest density in each spectrum = 1.0. Frequency in cycles/month. Equivalent periods unit (cycles/month)$^{-1}$

Colebrook (1977) studied the year-to-year fluctuations in biomass of 17 taxonomic categories in the California Current during 1955-59, using principal component analysis. The results of this study indicated that changes in biomass show a remarkable coherence among categories and among different geographic localities. In other words, a large element of the year-to-year fluctuations in biomass is common to all geographic areas in the region and to a vast majority of taxa. Although the increase in numbers of certain taxonomic categories at the expense of others could be explained by internal readjustments within the local ecosystem, such an explanation is untenable when all categories tend to increase or decrease their numbers simultaneously.

Indirect evidence that advection is playing a role can be inferred from changes of hydrographic characteristics between years of high and low biomass. As an indicator of advection of northern waters, from the subarctic and transitions zones, I have chosen the 33.40 °/oo isohaline at 10 m. This is a salinity value that characteristically lies in the middle of the halocline in the subarctic Pacific Ocean (Tully and Barber 1960). Toward lower latitudes

this isohaline approaches the surface layers of the ocean as the halocline itself becomes shallower, and at the surface it marks the midpoint of a zone of transition between the typical salinity structures of the subarctic and subtropical domains.

In order to summarize the information available, I have plotted the position of the 33.40 °/oo isohaline for all the months available in the years of interest (data from Anonymous 1963; Wyllie and Lynn 1971). The areal range of all observed positions of the 33.40 °/oo isohaline are presented in Figure 8 a and b. In a given year, the envelope usually defines an area to the north where the surface waters were always "fresher" than 33.40 °/oo and an equivalent area to the south and inshore where the surface waters were never "fresher" than 33.40 °/oo. The envelope itself is a conservative estimate, because in several cases the isohalines, during most of the year, were closely packed together and only a few extreme observations made the areal range wider. As a reference I have used the statistically determined position of the isohaline published by Lynn (1967).

The years 1950, 1953, and 1969 show intrusions of
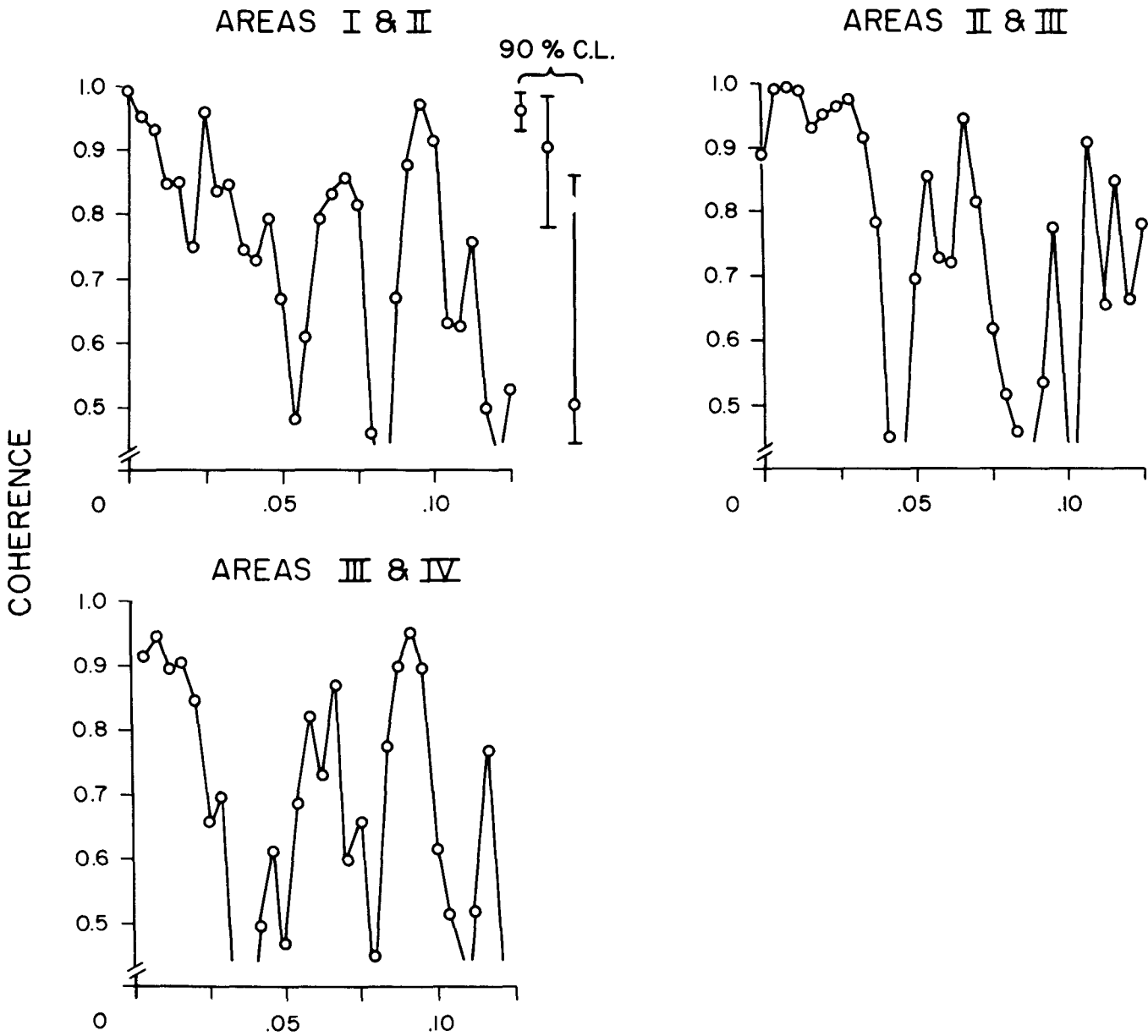
Figure 7. Spectral coherency plots for the three north-south area pairs. Coherence is a measure of the common variance between two series at any given frequency; 90% confidence limits for three selected values are presented beside the first plot. These limits were computed following the standard asymptotic approximations.

northern waters much farther south than the normal range. In 1958 and 1964 the isohalines did not appreciably extend further south than their average position. Although we used the salinity values at 10 m, these intrusions are not restricted to a thin surface layer. Figure 9 shows a time series of salinity versus depth for CalCOFI Station 90.60, located in Area II (32° 30' N, 120° W). Two major features are evident in the figure; the year-to-year variability and the depth range of northern waters, which extends to 100 m at this latitude. Thus, during the same years that anomalous biomass maxima or minima

were present, hydrographic changes could also be detected in the California Current.

Unfortunately a continuous record of nutrient concentration does not exist for the region, so that a direct quantitative comparison is not possible. Nonetheless, Zentara and Kamykowski (1977), analyzing the information available for the eastern Pacific Ocean, found that nitrate, phosphate, and silicate follow an inverse monotonic relationship with temperature. Between 65° N and 35° S, their nutrient scatter diagrams intercept the temperature axis, indicating nutrient depletion above cer-
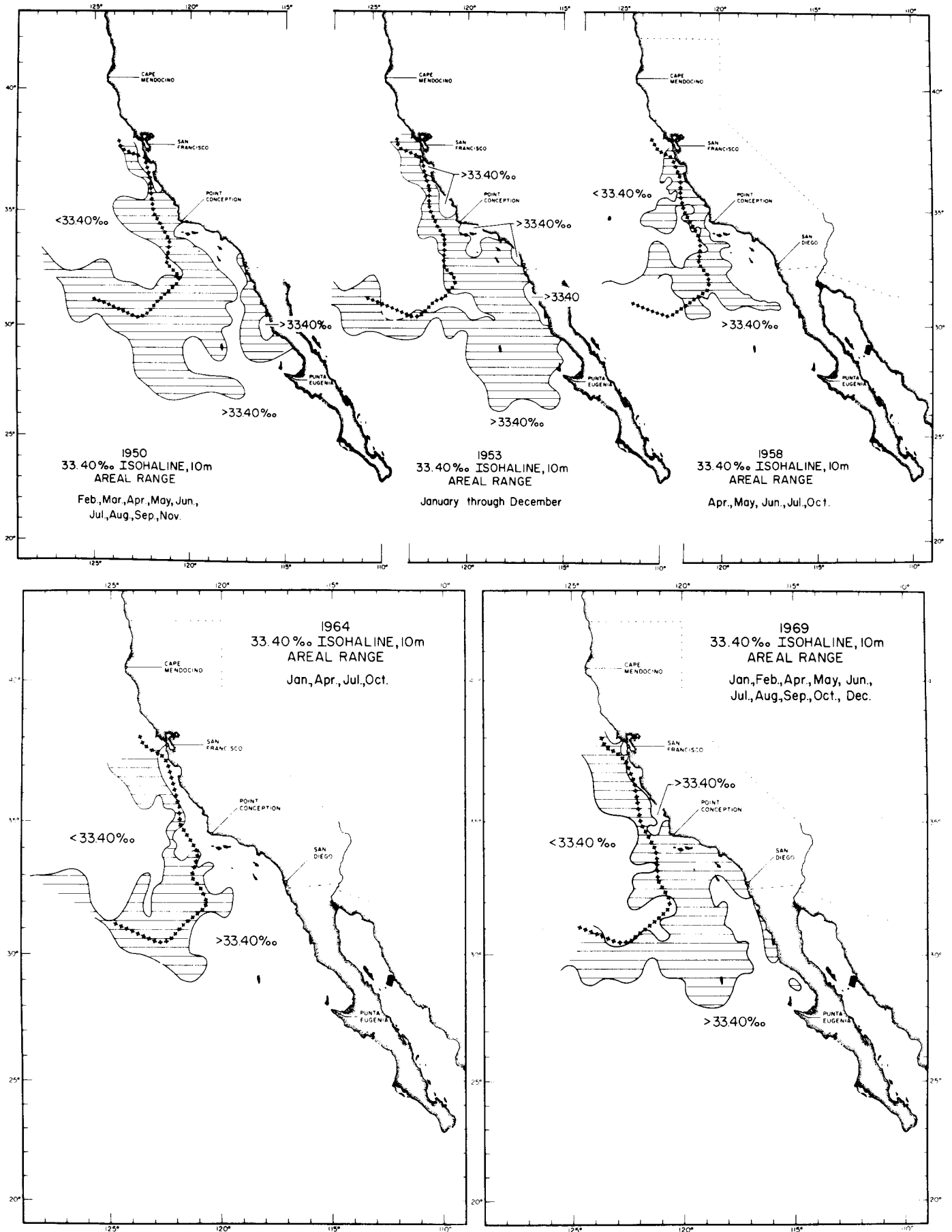
Figure 8. Extension of water masses of northern origin into the California Current. (a) Areal range of 33.40 °/oo isohaline for years 1950, 1953, and 1958. (b) Areal range of 33.40 °/oo isohaline for years 1964 and 1969. The stippled area includes all positions of the 33.40 °/oo isohaline observed for the period. The statistically computed average position of the isohaline is delineated by crosses.

TABLE 2.
Summary of Main Features of Five Discrete Events Characterized by Extensive Occurrence of Biomass Extremes over the California Current Region.

| Event	Area	Max/min value[1] ml/1000m[3]	# Extreme Values[2]	Run length[3] months	Run: Start/ End
1	I	1109.3 (5005)*	3 (5002, 03, 05)	11 (18)	4911-5104
	II	723.4 (5004)	3 (5002, 03, 04)	4	5002-5005
	III	279.2 (5004)	1 (5004)	4	5003-5006
2	I	642.9 (5308)	1 (5308)	4 (8)	5306-5401
	II	646.8 (5307)	4 (5306, 07, 08, 09)	18 (19)	5206-5312
	III	497.2 (5308)	2 (5307, 08)	7 (8)	5303-5310
	IV	170.5 (5310)	–	9	5302-5310
	V	91.0 (5308)	–	2	5307-5308
3	I	741.0 (5507)	1 (5507)	8 (22)	5408-5605
	II	506.7 (5607)	4 (5601, 07, 11, 5704)	14 (17)	5512-5704
	III	768.9 (5607)	7 (5512, 5601, 04, 05, 06, 07, 5702)	15 (18)	5512-5705
	IV	306.1 (5506)	8 (5404,5505,06,5604, 06,07,08,5703)	30 (36)	5404-5705
	V	437.9 (5605)	1 (5605)	....	....
4	I	123.1 (5806)	4 (5804,05,06,5810)	11 (18)	5711-5904
	II	25.4 (5901)	8 (5806,09,10,5901, 02,03,04,05,06)	31 (34)	5705-6002
	III	2.8 (5809)	9 (5807,08,09,10, 5902,03,04,05,06)	22 (24)	5802-6001
	IV	23.9 (5902)	2 (5810, 5902)	20 (24)	5803-6002
	V	20.7 (5804)	1 (5804)	4 (21)	5804-5912
5	II	315.1 (6410)	1 (6410)	5 (13)	6401-6501
	III	154.3 (6410)	1 (6410)	9 (25)	6301-6501
	V	120.3 (6407)	1 (6407)	3 (7)	6404-6410

[1]This is the maximum or minimum value of biomass within the run.
[2]Number of months above (below) ±9 codified units.
[3]Is the number of consecutive months above or below 21-year monthly means. In parentheses are given the numbers of months obtained by interpolation, assuming that blanks in the record had anomalies of the same sign.
*Cruises are identified by 4 digits; the first two indicate the year and the last two the month.

tain temperatures. A similar relationship has been reported for nitrate concentrations and ambient temperature (Strickland et al. 1970; Kamykowski 1973; Eppley et al. 1978). Typically the water mass lying to the north of the 33.40 $^\circ$/oo isohaline has temperature values well below these intercepts, less than 13° C between 40° and 35° N, for example, suggesting that it represents an important source of nutrients for the system.

There is also published evidence pointing to the importance of advection. Wickett (1967) found a positive correlation ($r = 0.84$; $p < 0.01$) between southward Ekman transport at 50° N and the zooplankton biomass off southern California one year later, suggesting that the zooplankton may be responding to a nutrient input taking place very far upstream. McGowan and Williams (1973) computed a budget of inorganic phosphorus for the subarctic Pacific and found an excess of 0.13 mg-atoms $PO_4/m^2/day$. Because there is no evidence that phosphorus is accumulating in the upper layers of the ocean at those latitudes, these authors concluded that the balance must be achieved by a net transport of phosphorus from the subarctic Pacific into the California Current. Colebrook (1977) concluded that "whatever influence or in-
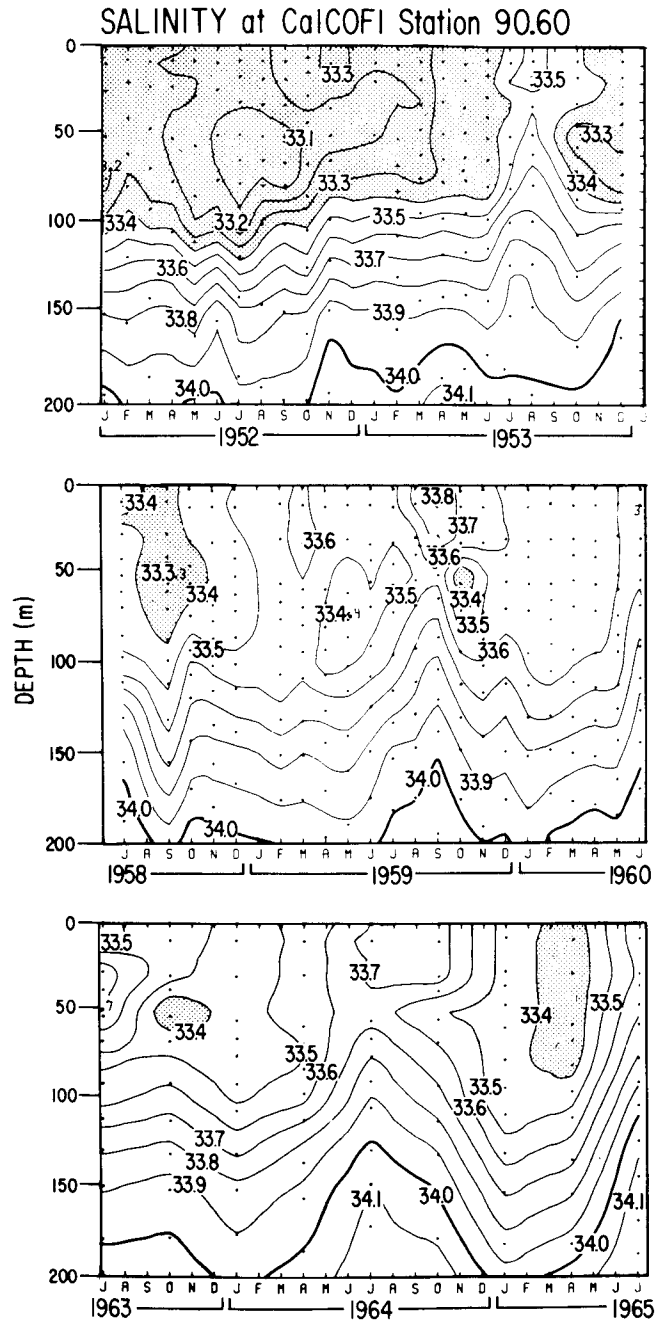
Figure 9. Time series of salinity versus depth at CalCOFI Station 90.60 (32° 30' N, 120° W) during some selected years. Salinities less than 33.40%$_o$ are stippled (Modified from Eber 1977).

fluences are responsible for the fluctuations in the plankton either have their origin in the north of the survey area or have a greater effect on those categories with northern patterns of distribution."

Other large-scale physical phenomena might also be playing an important role. Recent work by McCreary (1976), simulating the "El Niño" phenomenon, predicts that changes originating over the interior of the Pacific

Ocean in the equatorial region influence both eastern boundary currents, i.e. the Peru-Chile and California Currents. This phenomenon is accompanied by a deepening of the thermocline, a perturbation that according to the model travels poleward as coastally trapped Kelvin waves. In theory, according to the critical depth model (Sverdrup 1953), a deepening of the mixed layer, other things being equal, should result in a decrease of biological production. The zooplankton provides the first link in the marine food web, and a time lag in its response to this kind of external driving should be detectable.

In order to test this hypothesis, I have taken from Allison et al. (1971) a time series of quarterly sea-surface temperature anomalies computed for the equatorial band lying between 5° N-5° S and 80°-180° W. This series has been used as an indicator for "El Niños" events off the South American coast. By comparing it with the series of quarterly standardized anomalies of zooplankton biomass in Area III, I obtained a highly significant negative correlation ($r = -0.40; p < 0.01$) when the zooplankton lagged the temperature anomalies by three quarters (Figure 10). Although this evidence is not overwhelming, it is nonetheless an indication that some of the ecological events described, in particular the one occuring during the warm years of 1957 and 1958, might represent true "Californian El Niños." In any case, it indicates that McCreary's hypothesis deserves further study.

Figure 10. Californian "El Niños." Upper panel: Quarterly sea surface temperature anomalies for the equatorial band between 5° N - 5° S and 80° - 180° W. Well recognized "El Niños" events off Peru and Chile are shown as warm peaks (Allison et al. 1971). Lower panel: Codified standardized deviations of $\log_e$ zooplankton volume/quarter in Area III.

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APPENDIX

The absolute unit used by CalCOFI to report zooplankton displacement volumes is ml/1000 m³. Any standardized and codified value can be converted back to absolute units using the following relationship:

absolute value = (codified value × 0.2 × standard deviation) + mean

Because the codification transforms a continuous variable into discrete integers, some precision is lost due to rounding errors. This Appendix gives the necessary statistical parameters to perform such conversion. In the case of log-transformed series, the mean of $\log_e$ zooplankton volume corresponds to the geometric mean in absolute units. Symbols: "N" is the number of months with at least one observation, "$\overline{X}$" is the mean, "s" is the standard deviation, and G.M. is the geometric mean.

Zooplankton volumes:

	Area I	Area II	Area III	Area IV	Area V
N	115	164	162	155	91
$\overline{X}$	417.04	243.67	153.89	138.22	81.50
s	367.62	314.27	181.86	115.35	80.49

$\log_e$ zooplankton volumes:

N	115	164	162	155	91
$\overline{X}$	5.471	4.795	4.399	4.321	3.947
s	0.621	0.701	0.725	0.539	0.504
G.M.	237.70	120.90	81.37	75.26	51.78

Zooplankton volumes, N:

JAN	13	17	18	17	13
FEB	5	13	13	13	4
MAR	6	13	13	13	6
APR	16	18	19	19	14
MAY	13	14	13	13	9
JUN	14	16	16	14	8
JUL	17	19	19	19	12
AUG	8	10	11	11	7
SEP	4	10	12	11	5
OCT	11	16	15	15	8
NOV	5	9	5	4	3
DEC	3	9	8	6	2

Zooplankton volumes, $\overline{X}$:

	Area I	Area II	Area III	Area IV	Area V
JAN	227.76	137.59	94.42	79.84	92.87
FEB	281.77	338.97	107.30	91.04	179.25
MAR	308.33	329.50	121.90	102.70	148.76
APR	526.03	305.47	154.66	117.28	83.98
MAY	735.20	320.01	187.71	176.19	101.46
JUN	456.02	302.10	212.92	205.67	73.38
JUL	445.45	326.31	255.27	156.87	55.20
AUG	439.73	221.03	171.53	191.06	60.37
SEP	570.92	142.38	141.30	144.08	38.11
OCT	224.84	149.06	116.52	171.27	48.25
NOV	169.04	110.16	102.62	95.85	55.31
DEC	229.54	101.21	96.59	88.43	48.25

Log_e Zooplankton volumes, s:

	Area I	Area II	Area III	Area IV	Area V
JAN	0.419	0.528	0.560	0.421	0.512
FEB	0.793	0.721	0.456	0.485	0.241
MAR	0.722	0.649	0.605	0.576	0.518
APR	0.636	0.649	0.618	0.425	0.518
MAY	0.610	0.610	0.782	0.664	0.884
JUN	0.468	0.494	0.746	0.632	0.405
JUL	0.490	0.606	0.835	0.583	0.397
AUG	0.464	0.707	0.919	0.539	0.458
SEP	0.553	0.733	1.145	0.583	0.122
OCT	0.508	0.557	0.369	0.439	0.396
NOV	0.415	0.666	0.698	0.106	0.137
DEC	0.541	0.624	0.701	0.165	0.269

Zooplankton volumes, s:

	Area I	Area II	Area III	Area IV	Area V
JAN	145.99	72.31	79.42	35.69	64.76
FEB	339.13	618.27	58.78	58.38	148.37
MAR	325.69	502.91	74.30	66.39	120.69
APR	342.42	447.42	106.16	66.97	74.94
MAY	761.70	300.41	177.45	159.31	155.75
JUN	268.48	186.93	188.11	189.19	30.25
JUL	208.93	261.43	380.72	129.62	25.65
AUG	297.88	202.47	205.30	116.40	29.24
SEP	300.71	85.67	109.00	70.47	4.45
OCT	92.74	120.20	50.15	152.39	19.03
NOV	64.70	82.05	64.51	10.38	4.04
DEC	140.40	52.44	88.33	13.41	14.50

Log_e zooplankton volumes, G.M.

	Area I	Area II	Area III	Area IV	Area V
JAN	150.50	85.63	59.38	58.03	58.85
FEB	147.82	122.61	70.67	60.34	85.97
MAR	166.50	134.83	72.60	60.58	69.82
APR	294.71	143.02	85.54	68.99	49.35
MAY	341.38	161.58	98.20	78.65	52.19
JUN	304.60	179.47	116.16	79.36	58.50
JUL	315.76	184.20	103.13	74.14	46.02
AUG	286.86	132.82	86.75	116.86	48.52
SEP	276.44	93.88	71.81	93.50	35.76
OCT	163.20	90.65	80.64	95.20	42.27
NOV	140.47	68.17	62.99	75.79	51.31
DEC	151.71	64.07	59.98	74.29	40.85

Log_e Zooplankton volumes, $\overline{X}$:

	Area I	Area II	Area III	Area IV	Area V
JAN	5.014	4.450	4.084	4.061	4.075
FEB	4.996	4.809	4.258	4.100	4.454
MAR	5.115	4.904	4.285	4.104	4.246
APR	5.686	4.963	4.449	4.234	3.899
MAY	5.833	5.085	4.587	4.365	3.955
JUN	5.719	5.190	4.755	4.374	4.069
JUL	5.755	5.216	4.636	4.306	3.829
AUG	5.659	4.889	4.463	4.761	3.882
SEP	5.622	4.542	4.274	4.538	3.577
OCT	5.015	4.507	4.390	4.556	3.744
NOV	4.945	4.160	4.143	4.328	3.938
DEC	5.022	4.160	4.094	4.308	3.710

SEASONAL DISTRIBUTIONS OF EPIPELAGIC FISH SCHOOLS AND FISH BIOMASS OVER PORTIONS OF THE CALIFORNIA CURRENT REGION

ROGER P. HEWITT AND PAUL SMITH
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, CA 92038

ABSTRACT

Coarse distribution patterns of epipelagic fish schools over portions of the CalCOFI survey patterns are contrasted with estimates of biomass distribution patterns by season. Frequency distributions of fish-school sizes and peak target strengths are presented as well as the seasonal dependence in the position of these distributions. The data were collected on a series of six CalCOFI cruises during late 1974 and 1975.

INTRODUCTION

Sonar mapping yields rapid and efficient estimates of the numbers of epipelagic fish schools per unit area searched (Smith 1970; Mais 1974; Hewitt et al. 1976; Hewitt 1976; Fiedler 1978; Smith 1978). Estimates of mean school size are also possible and have been used to calculate the distribution pattern and abundance of schooled northern anchovy (*Engraulis mordax*) off the Californias (Mais 1974). Target strength measurements (indexing the ability of a school to reflect acoustic energy) have been made (Hewitt et al. 1976), but as yet an adequate understanding of the interaction between a pulse of sound and a dynamic array of scatterers does not exist to effect the incorporation of this parameter into an algorithm for the calculation of school biomass. On the other hand, fish distribution patterns inferred from the distribution of fish schools may be very misleading, i.e. it is not only possible but probable that a disproportionately large number of fish are in a small fraction of the schools

This report compares coarse distribution patterns of fish based on pooled counts of schools per unit area surveyed and that based on school biomass estimates, assuming the schools were all of northern anchovy. The data used were from that portion of the 1975 ichthyoplankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) conducted by the R/V *David Starr Jordan*.

METHOD

The primary objective of the CalCOFI survey cruises was to observe hydrographic and plankton tow stations. The station pattern is typically of lines 40 miles apart, approximately at right angles to the coast, and stations 20 to 40 miles apart along the lines. Also, during the 1975 cruises there was an intensification of station density in the Los Angeles Bight. On the other hand, our acoustic sampling technique requires that the ship be underway. Further, in an effort to avoid the unknown effects on schooling and detection of schools at night and twilight, we operated the equipment only between the hours of 0800 and 1600 (Smith 1970). These conditions contribute to a less-than-optimum design for a plankton survey cruise. However, survey design was not the primary concern; our motivation was the opportunity to collect sufficiently large amounts of data to allow us to further investigate and quantify sampling bases.

Figure 1 describes the transect coverage for all six cruises. There is some overlap between cruises; but the portion of the CalCOFI grid that was surveyed is clear.

Figure 2 is a schematic description of the survey configuration. A 30 kHz narrow beam sonar (10° between $-3dB$ downpoints) was directed at 90° from the ship's heading. The transducer was tilted down from the horizontal by 3° and transmitted 10 m sec pulses at 1-second intervals. The received signal was digitized at an interval corresponding to 1-m range and processed. Data recorded for each target included the time of detection, the mid-range of the target, the target size measured on a horizontal axis perpendicular to the ship's track, the peak target strength, and the number of sonar pings during which the target echo was detected (see Hewitt et al. 1976 for specific methodology). The ship's speed was also digitized and fed into the data processor, which interrupted data collection as the ship slowed to a stop and resumed data collection as the speed increased above a critical value. In this manner, acoustic data were collected along transects between CalCOFI stations. The range extent of the observation band was 250m—i.e. 200 to 450 m from the ship. Data from approximately 10,500 targets were logged during the six CalCOFI survey cruises.

RESULTS

Figure 3 describes the overall target size distribution for all cruises. The modal target size is about 45 m, and 50% of the targets are less than 50 m in size. The shape and position of this distribution is consistent with our
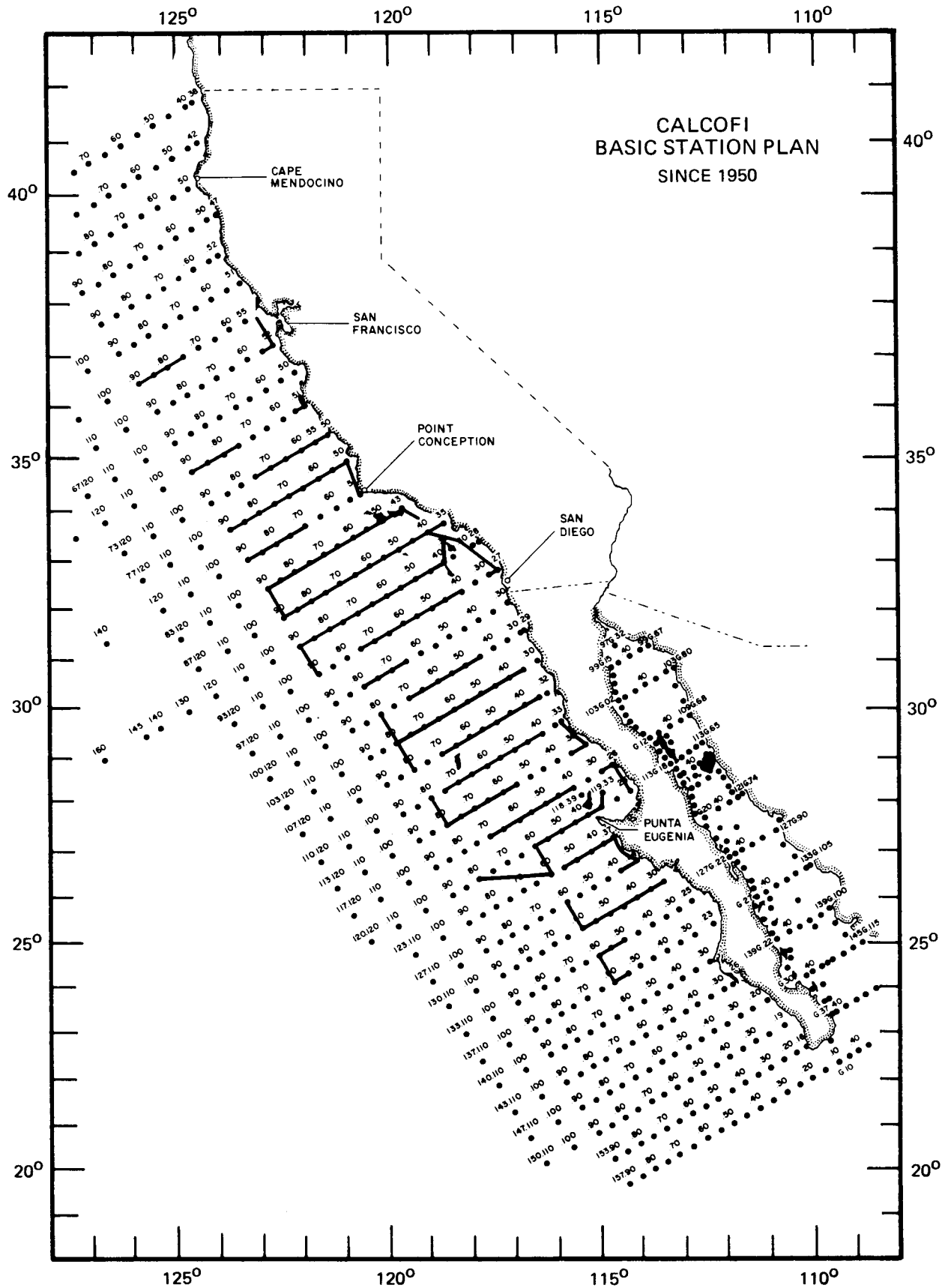
Figure 1. CalCOFI station pattern with sonar transect coverage for all cruises (from Vent et al. 1976).
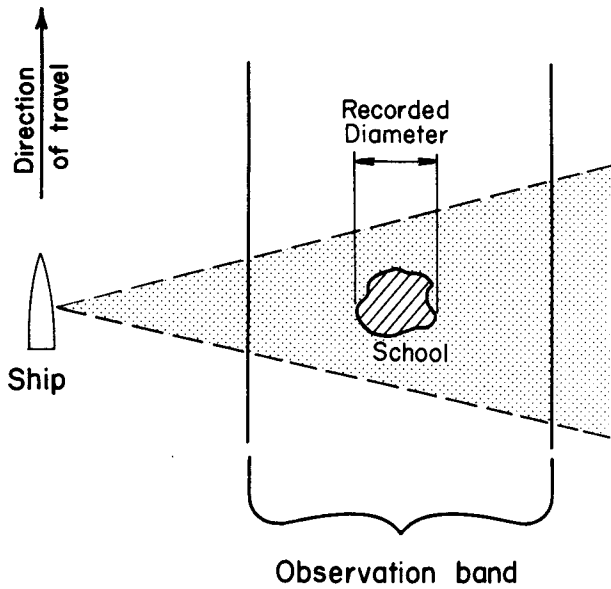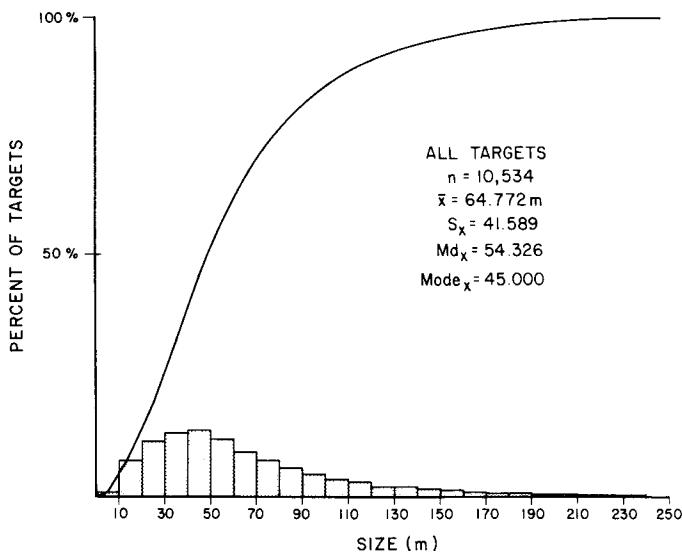
Figure 2. Plan view of the survey configuration.

Figure 3. Overall target size distribution with descriptive statistics.

Figure 4. Overall peak target strength distribution with descriptive statististics

where $\bar{x} = \frac{1}{n} \sum_{1}^{n} TS_i$ and $\bar{x}_{intensity} = 10 \log (\frac{1}{n} \sum_{1}^{n} antilog \frac{TS_i}{10})$; i.e. the geometric and arithmetic means of the power distribution.

Figure 5. Seasonal variation of target size (1974-75).

DISCUSSION

The major importance of target size and target strength measurements to a stock assessment technique is the contribution these values make to an estimate of the fish biomass in an individual school. The biomass model, developed below, involves several assumptions at each stage of its development.

First is the characterization of the echo received from an array of scatterers. Weston (1967) has addressed this problem by dividing the return into two components: a coherent component reflected from the boundary of a fish school and an incoherent component reflected by individual fish. Weston further showed that at frequencies far above resonance, the coherent component becomes negligible and the target strength of an array is the summation of the contribution of individual scatterers adjusted for the effects of multiple scattering and attenuation within the sample volume.

Resonance frequencies for the two dominant epipel-

previous experience.

Figure 4 describes the overall target strength distribution for all cruises. Here echo intensity is expressed in decibels, and the resulting distribution does not appear to be markedly skewed. The geometric mean of the power distribution is −7.8 dB and coincides with the modal target strength.

Figures 5 and 6 describe the variation of these values throughout the year. Target size was at a peak in the winter and declined steadily to a minimum in October 1975. Target strength appeared to peak in early winter and again in midsummer.
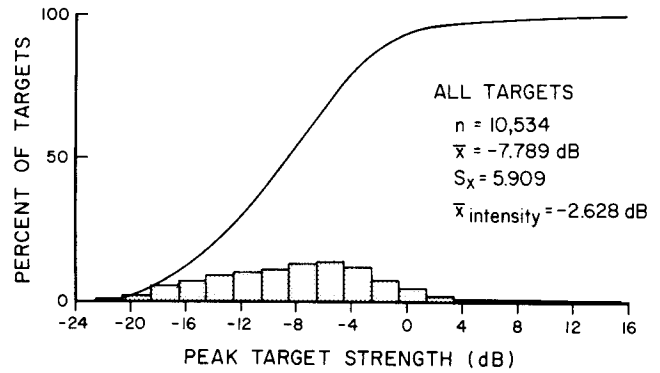
agic schooling species in the survey area, *Trachurus symmetricus* (jack mackerel) and *Engraulis mordax* (northern anchovy), have been reported to be near 1 kHz (Batzler and Pickwell 1970; Holliday 1972), which is well below the sonar operating frequency of 30 kHz. Thus, assuming only incoherent scattering, the acoustic scattering cross sections of *n* individuals within the sample volume are summed to equal the school target strength (*TS*):

$$(TS)_{school} = (TS)_{indiv} + 10 \log n$$

and

$$n = 10^{(\frac{TS_S - TS_i}{10})} \qquad (1)$$

We have assumed: 1) no multiple scattering of sound between fish or within the body of a single fish, and 2) negligible shadowing and attenuation of sound within the ensonified portion of the fish school. There is some support for this assumption from a Norwegian group (Røttingen 1976) who have measured a linear relationship between reflected acoustic energy and fish density over a moderate range of densities. It must be emphasized that this approach is a simplification, but a more rigorous model is premature. Using the present model, *n* may be expressed as a function of the school target strength and the target strength of an individual scatterer. However *n* represents the number of fish in the sample volume and not necessarily the entire school.

The sample volume is described in Figure 7 and may be approximated as the product of the *x*, *y*, and *z* dimensions. The *x* dimension is the range from which sound is received at any one instant; since we used an active sonar, we must account for a 2-way path and a pulse train of finite length. The *z* dimension is the vertical extent of the school; Mais (1974) has reported that we may expect considerably less variation in the vertical extent of fish schools as compared to their horizontal extent.
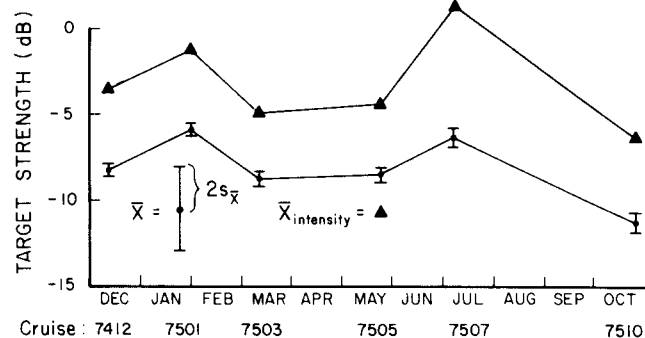
Figure 6. Seasonal variation of target strength (1974-75).
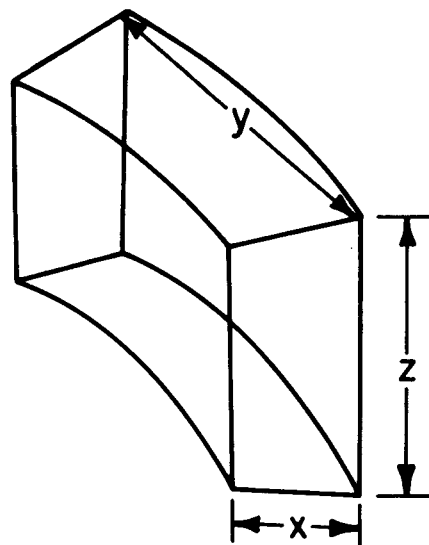
Where: $x = \dfrac{c\tau}{2} = \dfrac{1}{2}$ **pulse length**

$\left. \begin{array}{l} y = 2R \tan \beta \\ \text{or } (D_H) \end{array} \right\}$ **Whichever is less**

$z = D_V$

Figure 7. Estimation of the sample volume.

The *y* dimension is limited by beam geometry or by the size of the school if less than the horizontal beam width at the range of detection. In determining the value of *y*, we have used the target range extent (school dimension as an axis perpendicular to the ship's track) as an estimate of the school dimension on an axis parallel to the ship's track.

With respect to the estimation of the sample volume, we have assumed 1) the horizontal profiles of the schools are elliptical and randomly oriented, i.e. as more targets are measured during a survey, the error introduced by measuring one dimension becomes negligible; and 2) the vertical extent of fish schools in the upper mixed layer is entrely ensonified by the sonar beam. The former assumption apparently leads to a systematic overestimate (Squire 1978), and the latter may lead to an underestimate.

The sample volume is estimated as a product of *x, y,* and *z*. Thus, where the sample volume is limited by school size:

$$V = \frac{c\tau}{2} (D_H) (D_V) \qquad (2)$$

and where the volume is limited by beam geometry:

$$V = \frac{c\tau}{2} (2R \tan \beta)(D_V) \qquad (3)$$

where c is the speed of sound through water, τ is the pulse duration and $c\tau/2$ is one-half of the pulse length in m, D_V is the vertical extent of the fish school, D_H is the horizontal school size, R is the range of detection, β is the half beam angle and V is the sample volume in m^3.

The school biomass is estimated by applying the measured fish density to the entire school. The school shape is approximated by a cylinder of D_H diameter and D_V length. Thus,

$$B = \frac{n}{V} (\frac{\pi}{4}D_H^2)(D_V)(W_i) \qquad (4)$$

where B is the estimated school biomass and W_i is the weight of an individual fish.

At this point we have assumed 1) that the sample volume which yields the peak target strength is representative of the entire school, i.e. fish compaction is homogeneous throughout the school; and 2) that only fish of a similar weight are found within a single school.

By substituting equations (1), (2), and (3) into equation (4), two equations for the biomass of a school may be obtained that correspond to the limiting condition of the sample volume. For the case where sample volume is limited by school size

$$B = (k) 10^{(0.1 \, TS_S - 0.1 \, TS_i)}(D_H)(W_i) \qquad (5)$$

and where the sample volume is limited by beam geometry

$$B = (k') 10^{(0.1 \, TS_S - 0.1 \, TS_i)}(D_H)^2 (W_i)(R)^{-1} \qquad 6)$$

where k and k' are lumped constants. The school biomass may be thus expressed as a function of two measured variables: D_H (school size) and TS_S (peak school target strength) and two parameters that are specific to the species under study: W_i (weight of an individual) and TS_i (target strength of an individual). As a final note, D_H is reduced by one-half the pulse length ($c\tau/2$) to counter the increase in apparent range extent that occurs when a pulse train of finite length is used.

An idea of the sensitivity of the biomass estimate to assumed values for W_i and TS_i may be obtained by estimating the biomass of the most commonly observed school in terms of size and target strength (45 m, −7 dB) for various values of W_i and TS_i. for this purpose we will assume that the sample volume is limited by the school size. From an examination of Table 1, it is clear that the biomass estimate is much more sensitive to TS_i than W_i. As may be expected from an examination of equation (5), the biomass estimate changes in direct pro-

portion to W_i and by an order of magnitude for every 10 dB change in TS_i.

TABLE 1
Estimated Biomass (in metric tons).

W_i (in g)	TS_i (in dB)				
	−40	−45	−50	−55	−60
12	0.09	0.30	0.94	2.97	9.40
13	0.12	0.37	1.18	3.72	11.75
18	0.14	0.45	1.41	4.46	14.10
21	0.16	0.52	1.65	5.20	16.45
24	0.19	0.59	1.88	5.95	18.80

Conceivably an areal distribution of fish that is based on target size and target strength might be considerably different than one that is based solely on target counts. To see this effect we assumed that all of the schools were composed of adult anchovy with an individual weight of 18 g and an individual target strength of −50 dB.

Figure 8 shows the biomass frequency distribution for all of the targets encountered during the 1975 CalCOFI surveys. Ninety percent of the schools are 5 tons or less, and only 1% are greater than 45 tons.

Figures 9 through 13 compare the geographic distribution of fish as indicated by the number of targets detected per km^2 and by metric tons per km^2. It should be emphasized that these are coarse plots drawn from data points pooled over several 10's of km. As such, they are smoothed and do not represent the true contagion experienced in the distribution of fish schools.

Figure 9 was drawn from data collected in December 1974. The plot on the left describes the distribution of epipelagic fish schools in numbers per km^2. The contour interval is one school per km^2. Starting from Sebastian Viscaino Bay and proceeding northwest, there appears to be a monotonic increase in the numbers of schools per unit area. The plot on the right describes the distribution of estimated fish school biomass. Contour intervals are 5 metric tons per km^2, and the distribution pattern appears to be quite similar to the school distribution.

Figure 10 is drawn from data collected in January 1975. Here the comparison is somewhat different. The number of schools per unit area appears to be increasing with distance offshore, whereas the estimated biomass per unit area appears to increase in a south-to-north direction.

Figure 11 is compiled from data taken on a survey in March 1975. Although there appears to be a moderate concentration of schools offshore, the estimated biomass distribution has little relief. The relatively high concentration of estimated fish biomass in Sebastian Viscaino Bay is in contradiction to the distribution trends of fish schools.

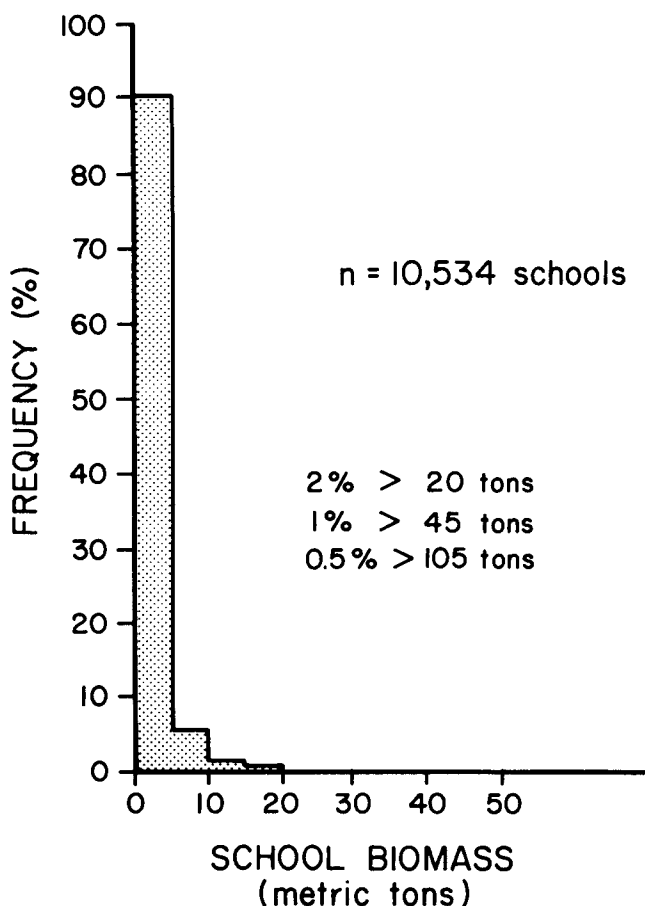Figure 12 describes data taken in May 1975. There is

Figure 8. Overall distribution of estimated school biomass.

sophisticated analysis, while certainly necessary, will not alter appreciably the basic results. It remains that a survey scheme that maps the occurrence of fish schools should acknowledge large between-school variations in fish packing density if it hopes to reproduce the distribution pattern of the fish.

A final note should be made of sampling biases, for which no attempt was made to correct but which we feel were constant enough so as not to change the qualitative results presented here. We have so far identified three major sources of systematic error: the first results from the use of a finite observation band where only those targets that lie entirely within the observation band are logged. As a consequence, large schools are undersampled relative to small ones because the range over which they may be detected is proportionately smaller. The second bias is caused by a range-dependent detection-rate loss, i.e. fewer targets are counted at longer ranges and the loss rate may vary seasonally and/or regionally. The third error arises from the fact that many schools are amoeboid-shaped (Squire 1978). By assuming school shape to be eliptical, we have overestimated the area of a school with any concave curvature of its perimeter. This effect may be examined with video tapes of school shapes taken with an airborne camera.

a concentration of fish schools per unit area offshore of northern Baja California and relatively few schools in the Los Angeles Bight. However, the distribution of estimated biomass per unit area shows the highest concentration in the inshore portion of the Los Angeles Bight.

Figure 13 is from data taken on the July 1975 CalCOFI cruise. Here relatively few numbers of fish schools were estimated to contain a relatively large amount of fish biomass. The highest concentration of estimated biomass per unit area is inshore.

The October 1975 cruise was not plotted, because it was conducted over too small an area. If a simple integration of biomass per unit area over area surveyed were performed and then normalized to counter the effect of unequal survey effort, the results would show the highest estimates of biomass in the months of January 1975 and July 1975.

The message contained in these plots is clear: the distribution (and abundance) of a target species inferred from the density of schools per unit area may be seriously midleading. Admittedly, these are coarse plots based on a crude biomass model, but we believe that a more

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SONAR TARGETS/SQ KM 7412

METRIC TONS/SQ KM 7412
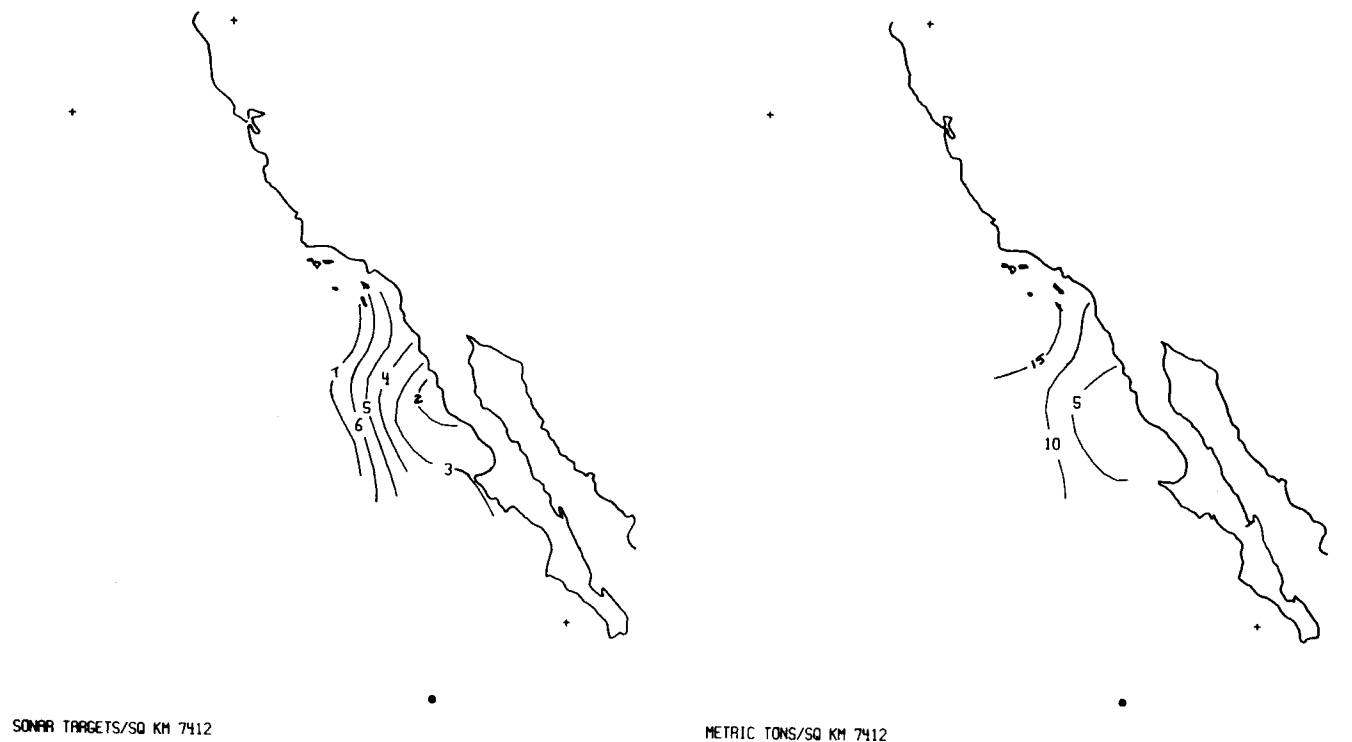
Figure 9. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7412 (December 1974).

SONAR TARGETS/SQ KM 7501

METRIC TONS/SQ KM 7501

Figure 10. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7501 (January 1975).

SONAR TARGETS/SQ KM 7503

METRIC TONS/SQ KM 7503

Figure 11. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7503 (March 1975).

SONAR TARGETS/SQ KM 7505

METRIC TONS/SQ KM 7505

Figure 12. Geographic distribution pattern of schools and estimated fish biomass during cruise 7505 (May 1975).

SONAR TARGETS/SQ KM 7507

METRIC TONS/SQ KM 7507
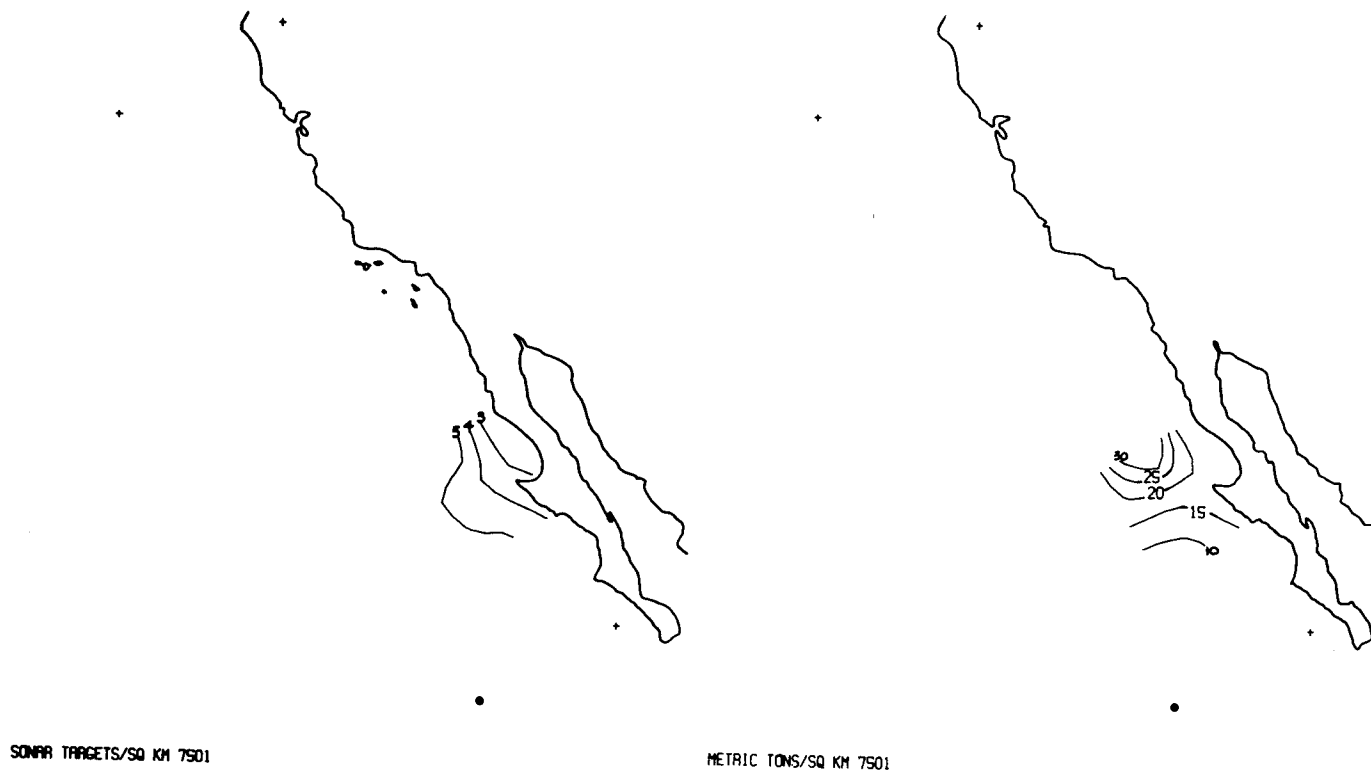
Figure 13. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7507 (July 1976).

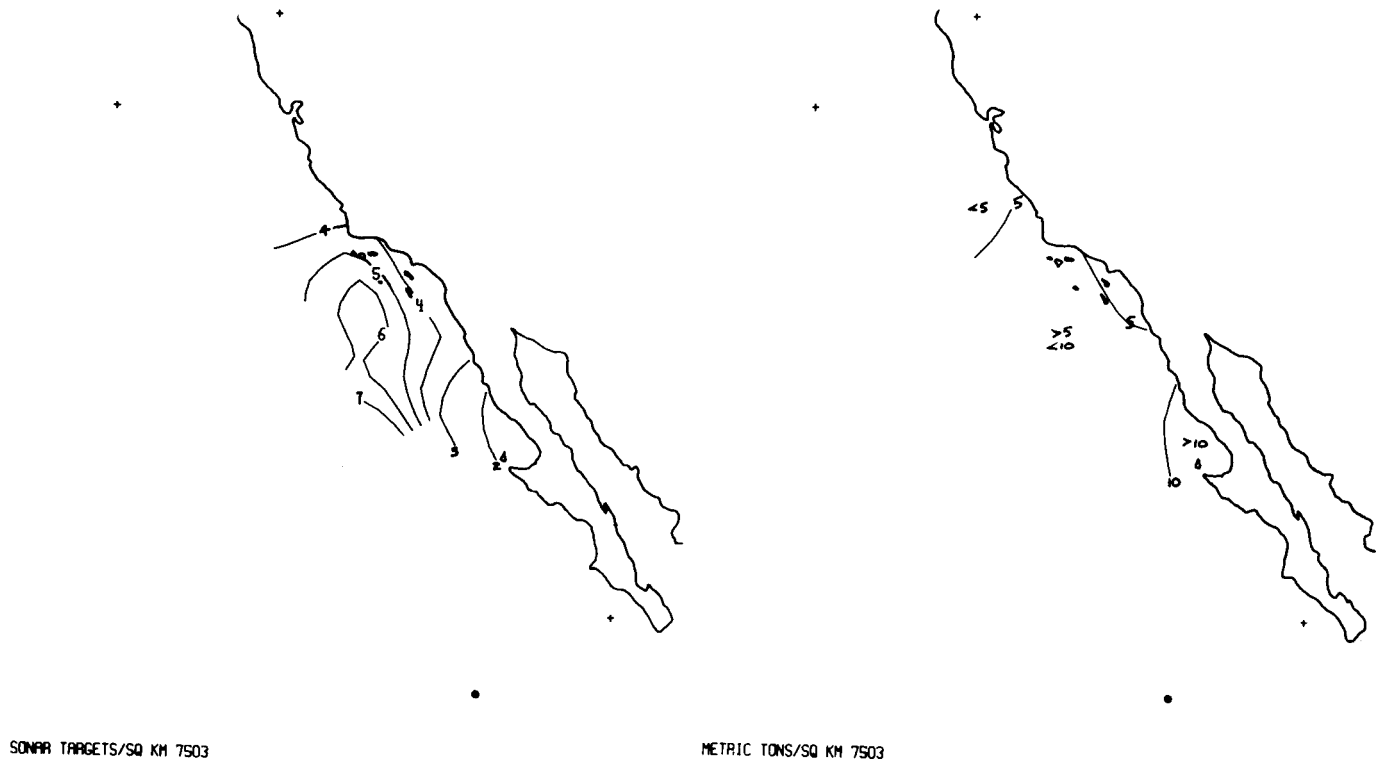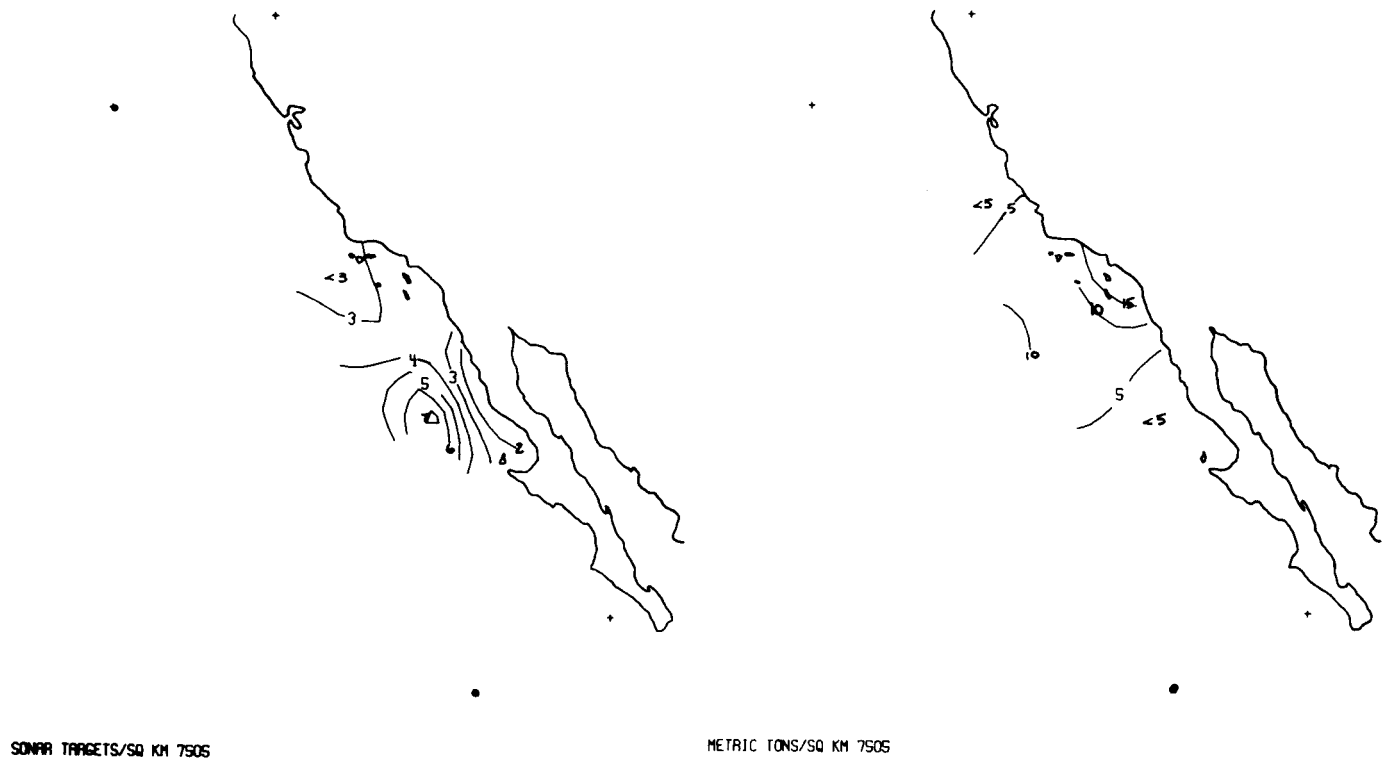# ABUNDANCE, COMPOSITION, AND RECRUITMENT OF NEARSHORE FISH ASSEMBLAGES ON THE SOUTHERN CALIFORNIA MAINLAND SHELF.

ALAN J. MEARNS
Southern California Coastal Water Research Project
1500 East Imperial Highway
El Segundo, CA 90245

ABSTRACT

Data on coastal fishes taken during a 8-year time-series of trawl surveys of northern Orange County (southern San Pedro Bay), California, were examined to determine how variable catches have been and whether or not they have changed in accordance with variations in such basic oceanographic conditions as temperature and transparency. Nearly 120,000 specimens of more than 112 species of fishes, sharks, and rays, and an equally large number of shrimp, crabs, echinoderms, and other invertebrates were collected during the quarterly trawl surveys at depths between 18 and 200 m. During this period (1969-77), fish abundance in the survey area varied about 4-fold. The variation was largely due to episodic recruitment of mixed assemblages of juvenile fishes. Most episodes of recruitment to the coastal shelf occurred during the onset of increasing turbidity and just following the coldest periods of the year. Alternating years of strong and weak year classes of rockfish and other species were observed and appeared to be directly influenced by oceanographic conditions.

It is suggested that further analysis of these and other coastal trawl survey records might help in understanding dynamics of mixed species populations and offer insight into approaches for assessment of multispecies management problems.

INTRODUCTION

For many years a number of local government agencies have conducted coastal fish surveys using small, fine-mesh, otter trawls at depths ranging from 5 to more than 200 m. In southern California, these surveys have produced a large amount of data on the abundance, distribution, health, and diversity of more than 150 species of marine fishes (Southern California Coastal Water Research Project 1973; Allen and Voglin 1976). Analysis of some of these data has helped identify disease epicenters (Mearns and Sherwood 1974) and some important features of structure and depth zonation of mainland shelf fish assemblages (Mearns 1974; Mearns and Smith 1976; Allen 1977a). However, much of the data from these and ongoing surveys remains unanalyzed and unused by fishery biologists. This is partly because, in the past, trawls have not been considered particularly quantitative or efficient sampling tools and partly because many fishery biologists may not be aware of the kind and quality of data that is now being taken in coastal monitoring programs.

The purpose of this paper is, first, to demonstrate the kind of analyses that are possible from contemporary local trawl surveys and, second, to identify some possible sources and causes of year-to-year variation in catches of nearshore fish populations.

My analyses are based on data from an 8-year time-series of quarterly trawl surveys conducted in southern San Pedro Bay off Orange County. Early in the work, it became apparent that year-to-year differences in the recruitment, growth, and survival of juvenile fishes were primarily responsible for year-to-year differences in total catch. Thus, I focused attention on young fishes and their particular relationship to variations in oceanographic conditions.

A major question now facing many local government agencies is: How much sampling is enough? Thus, I have also included in this report a retrospective analysis of the kind of information acquired during consecutive years of trawling at this particular site.

METHODS

This study is based on analysis of data on fishes captured during an 8-year time-series of trawl surveys on the mainland shelf in southern San Pedro Bay off northern Orange County, California (Figure 1). This part of the mainland shelf is characterized inshore (20 m) by a silty-sand soft bottom, grading offshore (to 100 m) to a soft bottom composed of sandy silt and olive-green mud. Centers of hard-bottom substrate inshore include an artificial sportfishing reef, power plant intake and discharge lines (at Huntington Beach), and an abandoned 1.6-km (1-mile) sewage outfall. Located offshore are an oil platform and the terminus of an active 8-km (5-mile) wastewater outfall, operated by the County Sanitation Districts of Orange County (CSDOC). This outfall began operation in 1971 and discharges 180 million gallon/day of primary-treated domestic sewage through a long, multiport diffuser located at a depth of 60 m. As described elsewhere (Mearns et al. 1976; Pamson et al. 1978), the principle effect of the outfalls has been to increase the relative abundance of several flatfish species at a station closest to the new outfall and to reduce fish abundance at a shallower site near an outfall abandoned in 1971.

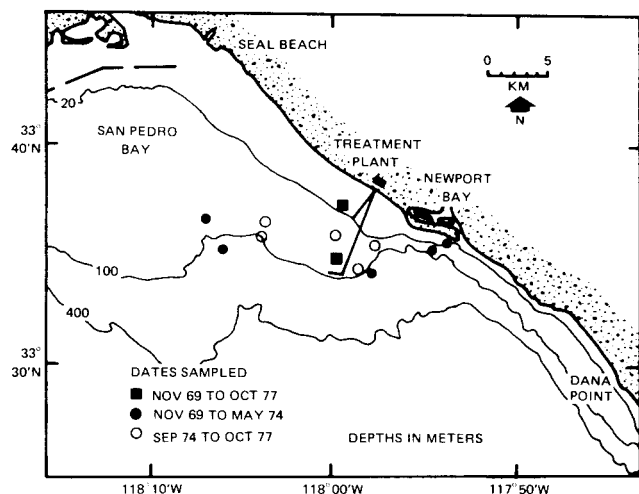The quarterly trawl program was initiated in August

Figure 1. Trawl survey stations in southern San Pedro Bay, California, 1969 through 1977.

1969 by Marine Biological Consultants, Inc., of Costa Mesa under contract to the Orange County Sanitation Districts (OCSD). Six stations were sampled that month (20-60 m). Beginning in November, a fixed grid of eight stations (20-170 m) was sampled, with 1 haul/station, quarterly through May 1974. In 1974, the Santa Ana Regional Water Quality Control Board ordered a change in location of several stations and deletion of the deepest. Quarterly trawling has continued at these seven fixed stations with an occasional deep trawl (170 m) as ship time permits. Stations and their changes are shown in Figure 1.

Important changes taking place during the survey period included 1) a change of vessels (*Fury II* to *Van Tuna*) in August 1970, and 2) diversion of effluent (at the time 130 MGD) from a shallow (18 m) 1-mile outfall to the deep (58 m) 5-mile outfall in April 1971. Beginning in November 1971, biologists from this project have participated in all but one survey.

A 7.6-m (25-foot) head rope-length otter trawl fitted with a 3.8-cm (1½-inch) stretch mesh bag and a 1.3-cm (½-inch) stretch mesh cod end was used in all surveys. Detailed characteristics of this gear were reported by Mearns and Stubbs (1974). On most occasions, the net was towed with a pair of 14-m (46-foot) bridles. Measurements at sea confirmed that the nets were opening 4.9-5.2 m (16-17 feet, door spread) during towing.

Trawls were taken along isobaths and generally down-swell. Boat speed during trawling was 4.6 km/hour (2.5 knots). Trawls were ten minutes in duration, measured from the time the cable was fully deployed to the time retrieval was begun. In actual practice this meant that the trawl was probably on bottom somewhat longer (e.g. up to 15 minutes). Scope ratios used on the *Van Tuna* were high, ranging from 8:1 at 18 m, 4 or 5:1 at 46-55 m, to

3.3:1 at 90 m.

Upon retrieval, all animals were sorted and larger organisms identified and counted. Most fishes were readily identified in the field, but juvenile rockfishes and sanddabs (*Citharichthys*) required special examination (Allen 1976, 1977b). Beginning in 1969 fishes were examined for external diseases, and the range of sizes (largest and smallest) were reported. Beginning in 1971 all fishes were measured to the nearest cm standard length (SL), and beginning in 1975 fishes and invertebrates were weighed in lots by species.

Marine Biological Consultants, Inc. (1974) published quarterly and annual reports of the total catches through May 1974, with CSDOC taking over this task beginning with the September 1974 survey. Data taken on all fishes have been coded, keypunched, and summarized in a computer format by the Southern California Coastal Water Research Project (SCCWRP). For my analysis, I considered each survey as a unit of effort for examining long-term trends and each sample within a survey for examining variation within that survey.

RESULTS

Catch Composition

Over 119, 700 fishes, representing 112+ species and 37 families of sharks, rays, and bony fishes were collected in the 258 samples taken between August 1969 and October 1977. The rather diverse fauna (Table 1) was dominated by rockfishes (Scorpaenidae, 25+ species), pleuronectid flatfishes (10+ species), surfperch and sea perch (Embiotocidae, 8 species), bothid flatfish (7+ species) and sculpins (Cottidae, 7+ species). Other well-represented families included the cusk eels and eelpouts (Ophidiidae and Zoarcidae), the greenling family (Hexagrammidae), poachers (Agonidae), and croakers (Sciaenidae). The most abundant and most frequently occurring species throughout the period (summarized in Table 2) included the speckled and Pacific sanddabs (*Citharichthys stigmaeus* and *C. sordidus*, respectively), yellowchin sculpin (*Icelinus quadriseriatus*), and Dover sole (*Microstomus pacificus*). These as well as the bigmouth sole (*Hippoglossina stomata*), English sole (*Parophrys vetulus*), horny-head turbot (*Pleuronichthys verticalis*), and the California tonguefish (*Symphurus atricauda*) were present in all surveys.

Young and adult fish of a number of economically important species were captured in these surveys. As shown in Table 3, there were frequent catches of northern anchovy (*Engraulis mordax*), California scorpionfish (*Scorpaena guttata*), petrale sole (*Eopsetta jordani*), chilipepper (*Sebastes goodei*), California halibut (*Paralichthys californicus*), cow rockfish (*Sebastes levis*),

Scientific Name	Common Name	Total Number Caught	Occurrence in Surveys (34)
Myxinidae			
Eptatratus stouti	Pacific hagfish	1	1
Carcharhinidae			
Mustelus californicus	Gray smoothhound	3	2
Squalidea			
Squalus acanthias	Spiny dogfish	25	6
Rhinobatidae			
Platyrhinoides triseriata	Thornback	5	2
Rhinobatos productus	Snovelnose guitarfish	15	6
Torpidinidae			
Torpedo californica	Pacific electric ray	10	9
Rajidae			
Raja kincaidi	Sandpaper skate	3	3
Myliobatidae			
Myliobatis californica	Bat ray	1	1
Chimaeridae			
Hydrolagus collei	Ratfish	12	8
Ophichthidae			
Ophichthus zophochir	Yellow snake eel	1	1
Engraulidae			
Anchoa compressa	Deepbody anchovy	12	1
Engraulis mordax	Northern anchovy	1,566	16
Argentinidae			
Argentine sialis	Pacific argentine	39	3
Synodontidae			
Synodus lucioceps	California lizardfish	561	22
Batrachoididae			
Porichthys myriaster	Specklefin midshipman	127	19
Porichthys notatus	Plainfin midshipman	4,503	32
Moridae			
Physiculus rastrelliger	Hundredfathom codling	13	4
Merlucciidae			
Merluccius productus	Pacific hake	62	11
Ophidiidae			
Chilara taylori	Spotted cusk eel	252	27
Otophidium scrippsae	Basketweave cusk eel	14	6
Otophidium sp.		2	2
Zoarcidae			
Aprodon cortezianus	Bigfin eelpout	65	5
Lycodopsus pacifica	Blackbelly eelpout	1,961	26
Lyconema barbatum	Bearded eelpout	95	9
Sygnathidae			
Sygnathus californiensis	Kelp pipefish	25	11
Sygnathus exilis		18	7

Scientific Name	Common Name	Total Number Caught	Occurrence in Surveys (34)
Scorpænidae			
Scorpaena guttata	California scorpionfish	312	29
Sebastes chlorostictus	Greenspotted rockfish	20	5
Sebastes crameri	Darkblotched rockfish	95	8
Sebastes dalli	Calico rockfish	5,768	31
Sebastes diploproa	Splitnose rockfish	1,491	17
Sebastes elongatus	Greenstriped rockfish	10	9
Sebastes eos	Pink rockfish	3	2
Sebastes flavidus	Yellowtail rockfish	6	1
Sebastes goodei	Chilipepper	177	13
Sebastes hopkinsi	Squarespot rockfish	1	1
Sebastes jordani	Shortbelly rockfish	128	12
Sebastes levis	Cow rockfish	93	20
Sebastes miniatus	Vermillion rockfish	287	25
Sebastes mystinus	Blue rockfish	37	8
Sebastes paucispinus	Boccacio	48	11
Sebastes rosaceus	Rosy rockfish	37	4
Sebastes rosenblatti	Greenblotched rockfish	31	13
Sebastes rubrivinctus	Flag rockfish	48	20
Sebastes saxicola	Stripetail rockfish	6,888	27
Sebastes semicinctus	Halfbanded rockfish	4,019	29
Sebastes serranoides	Olive rockfish	7	5
Sebastes serriceps	Treefish	1	1
Sebastes umbrosus	Honeycomb rockfish	5	3
Sebastes vexillaris	Whitebelly rockfish	3	3
Sebastes sp. (unid.)		7	4
Sebastes (Sebastomus) sp. (unid.)		2	2
Sebastolobus alascanus	Shortspine thornyhead	122	8
Hexagrammidae			
Ophiodon elongatus	Lingcod	3	3
Oxylebius pictus	Painted greenling	5	5
Zaniolepis frenata	Shortspine combfish	632	26
Zaniolepis latipinnis	Longspine combfish	1,571	32
Anoplopomatidae			
Anoplopoma fimbria	Sablefish	58	18
Cottidae			
Artedius notospilotus	Bonyhead sculpin	1	1
Chitonotus pugetensis	Roughback sculpin	1,582	28
Icelinus quadriseriatus	Yellowchin sculpin	12,728	34
Icelinus tenuis	Spotfin sculpin	5	1
Leptocottus armatus	Pacific staghorn sculpin	15	4
Radulinus asprellus	Slim sculpin	37	5
Scorpaenichthys marmoratus	Cabezon	2	2
Cottidae, unid.		1	1
Agonidae			
Agonopsis sterletus	Southern spearnose poacher	18	8
Odontopyxis trispinosa	Pygmy poacher	291	33
Xeneretmus latifrons	Blacktip poacher	779	15
Xeneretmus triacanthus	Bluespotted poacher	56	12
Percichthyidae			
Stereolepis gigas	Giant sea bass	1	1
Serranidae			
Paralabrax maculato-fasciatus	Spotted sandbass	4	2
Paralabrax nebulifer	Barred sandbass	7	5

Scientific Name	Common Name	Total Number Caught	Occurrence in Surveys (34)
Branchiostegidae			
Caulolatilus princeps	Ocean whitefish	13	7
Sciaenidae			
Cheilotrema saturnum	Black croaker	3	3
Genyonemus lineatus	White croaker	6,371	33
Menticirrhus undulatus	California corbina	13	9
Seriphus politus	Queenfish	1,546	23
Embiotocidae			
Amphistichus argenteus	Barred surfperch	3	3
Cymatogaster aggregata	Shiner perch	986	26
Embiotoca jacksoni	Black perch	110	22
Hyperprosopon argenteum	Walleye surfperch	112	15
Phanerodon furcatus	White seaperch	385	30
Rhacochilus toxotes	Rubberlip seaperch	7	4
Rhacochilus vacca	Pile perch	8	9
Zalembius rosaceus	Pink seaperch	3,446	33
Bathymasteridae			
Rathbunella sp. A	Bluebanded ronquil	8	3
Rathbunella hypoplecta	Smooth ronquil	12	4
Uranoscopidae			
Kathetostoma averruncus	Smooth stargazer	15	7
Clinidae			
Neoclinus blanchardi	Sarcastic fringehead	1	1
Stichaeidae			
Plectobranchus evides	Bluebarred prickleback	4	3
Poroclinus rothcocki	Whitebarred prickleback	2	1
Gobiidae			
Coryphopterus nicholsi	Blackeye goby	25	8
Lepidogobius lepidus	Bay goby	67	22

Scientific Name	Common Name	Total Number Caught	Occurrence in Surveys (34)
Trichiuridae			
Lepidopus xantusi	Pacific scabbard fish	1	1
Stromateidae			
Icichthyes lockingtoni	Medusa fish	5	3
Peprilus simillimus	Pacific pompano	73	9
Bothidae			
Citharichthys fragilus	Gulf sanddab	150	7
Citharichthys sordidus	Pacific sanddab	16,742	34
Citharichthys stigmaeus	Speckled sanddab	20,485	34
Citharichthys xanthostigma	Longfin sanddab	449	26
Citharichthys unid.		55	1
Hippoglossina stomata	Bigmouth sole	539	34
Paralichthys californicus	California halibut	146	29
Xystreurys liolepis	Fantail sole	53	15
Pleuronectidae			
Eopsetta jordani	Petrale sole	268	6
Glyptocephalus zachirus	Rex sole	1,605	20
Hypsetta guttulata	Diamond turbot	48	13
Lyopsetta exilis	Slender sole	2,606	21
Microstomus pacificus	Dover sole	7,436	34
Parophrys vetulus	English sole	2,182	34
Pleoronichthys coenosus	C-O sole	37	15
Pleuronichthys decurrens	Curlfin sole	323	24
Pleuronichthys ritteri	Spotted turbot	11	8
Pleuronichthys verticalis	Hornyhead turbot	891	34
Pleuronichthys unid.		2	2
Pleuronectiformes unid.		54	2
Cynoglossidae			
Symphurus atricauda	California tonguefish	5,633	34
		Total 119,764	

Pacific hake (*Merluccius productus*), and sablefish (*Anoplopoma fimbria*). A young giant sea bass (*Stereolepis gigas*) was also captured in one trawl.

Species and their relative abundances are similar to those reported from Santa Monica Bay by Carlisle (1969).

Catch Statistics

Overall, the average haul in these surveys took 15.9 species and 469 specimens with a Shannon-Weaver diversity of 1.62 (Table 4). Previous calculations indicated that average fish biomass in these hauls was 10.7 ± 4.4 (standard error) kg (Allen and Voglin 1976). Single surveys (of 7 or 8 hauls) actually took from 1570-6344 fish (average 3544) and 23-65 (average 44.1) species. Comparison of catch parameters using coefficients of variation (CV) of survey means indicated that Shannon-Weaver diversity and number-of-species per haul were the least variable parameters (CV = 12.3 and 18.5%, respectively) and that total number-of-fish per haul was the most variable (ranging from CV = 27.7% for catch-minus-smallest fish to 71.8% for the small fish alone, Table 4). These "between survey" variations were considerably lower than "within survey" variations caused

by differences among individual samples. In fact, co-efficients of variation within surveys averaged 25.1% for diversity, 26.3% for number-of-species per haul, and 62% for total-catch per haul. Thus the survey as a unit of effort was about one-half as variable as a single haul as a unit of effort.

Long-Term Trends and Species Acquisition

As indicated in Figures 2a, b, and c, average catch per unit effort, diversity, and number-of-species per haul underwent both seasonal and longer-term episodes of increases and decreases. Largest catches (500-800 fish/haul) occurred in 1969, 1971, 1973, 1974, 1975, and 1977; there were extremely low catches (less than 300 fish/haul) in 1970 and again in 1976. The extremes in total catch were only partially accompanied by similar fluctuations in Shannon-Weaver diversity and number-of-species per haul (especially from 1975 onward). Diversity was higher in 1971, 1972, 1973, 1975, and 1977, lower in other years, with peak values occurring in the spring or early summer.

Species acquisition curves are frequently used to evaluate the completeness of sampling programs in describing
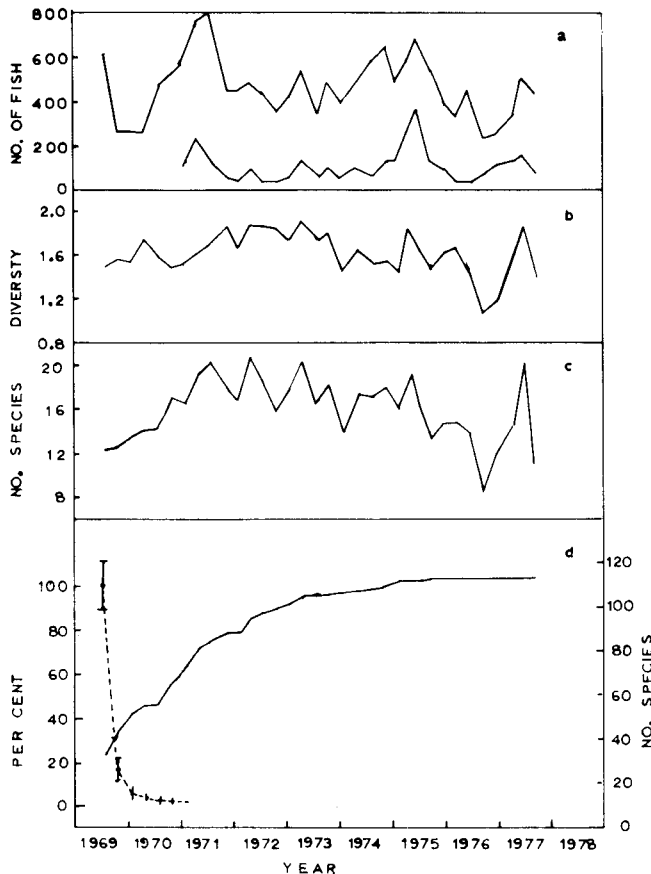
Figure 2. Fluctuations in (a) average catch per haul for all fish (upper line) and for fish ≦ 55 mm standard length (lower line); (b) Shannon-Weaver diversity index (c) average number-of-fish-species per haul for 34 quarterly surveys. Lowest figure (d) shows species acquisition curve (solid line) and percent of catch composed of new species averaged from six surveys drawn at random from the data (dashed line).

the fauna present at a given locality. As shown in Figure 2d, acquisition of the 112 species required about six years of quarterly surveys; approximately 30% of these were encountered in the first survey (representing 2.3% of the samples); by the fifth survey (15% of the samples, 1¼ years into the time series), approximately 50% of the species were encountered, and by the 15th survey, 90% of the species were acquired. At present, new species are being encountered at a rate of less than 1/year. This indicates that the ichthyofauna at this site has been more than adequately described within six years of quarterly trawling.

A second approach, using what may be termed a "species-abundance curve" (after a procedure in Word 1977), indicates that acquisition of those species that account for most of the abundance occurred at a much faster rate than species acquisition alone (Figure 2d). For example, at the second survey, 15% of the individuals were represented by new species added by that survey. In the fourth survey, less than 3% of the specimens were represented by newly acquired species, and by the sixth

survey new species contributed less than 2% to total abundance. Extrapolation indicates that two years of quarterly trawling were sufficient to encounter those species responsible for 99% of the total catch.

Juveniles as Source of Variations

As shown in Table 4 and in Figure 2a, large fluctuations in the catch of very young fish (≤ 55 mm standard length [SL]) was one factor contributing to year-to-year differences in total catch. For most of these species, fish 5.5 cm (SL) or less in size are only a few months old, and fluctuations in their abundance probably represent their success in recruiting into, and surviving in, the survey area. As indicated above, the coefficient of variation for average survey catches of these small fish was high (78%; Table 4); occasionally catches of these "young of the year" accounted for one-half of the total catch (average 20%; range 7.2-55.4%), and over half (69) of the 112 species (62%) were at one time or another represented by their young. However, as shown in the last column of Table 2, 28 common and abundant species were not equally represented by their young. Young of the speckled and Pacific sanddabs, yellowchin sculpin, pink sea perch (*Zalembius rosaceus*), and stripetail rockfish were present in 70% or more of the surveys. Common and abundant species such as white croaker (*Genyonemus lineatus*), calico rockfish (*Sebastes dalli*), English sole (*Parophrys vetulus*), northern anchovy (*Engraulis mordax*), queenfish (*Seriphus politus*), and shiner perch (*Cymatogaster aggregata*) were only occasionally represented by their young (8.8-34% of the surveys), suggesting that the primary rearing or brooding areas were located outside this survey area (i.e. inshore or offshore or in nearby bays and estuaries). In other words, most of the fishes of these species caught were somewhat older migrants from elsewhere. Low frequencies of occurrence of several deepwater species (such as rex sole [*Glyptocephalus zachirus*]) were due in part to deletion of one deep water station in 1974.

Recruitment Patterns

As summarized in Figure 3a, young fish appeared in abundance in the survey area on only a few episodic occasions during the 8-year period. Largest catches occurred during the spring and early summer of 1975 when more than 4,500 young (50% of the total catch) of more than 20 species were caught. The next largest periods of "recruitment" detected occurred in the winter or spring of 1971. The years 1972, 1974, and 1976 showed rather poor catches of young fish.

Periods of "recruitment" were not due only to single species. The average number of species represented by specimens ≤55 mm SL was 12.7; however, during major

115

TABLE 2

Percent Abundance and Frequency of 28 Fish Species that Account for 96% of the Catch in 34 Quarterly Trawl Surveys off Orange County, August 1969 through October 1977.*

Common Name	% of Total Catch	Frequencies of Occurrence in Surveys	
		All fish	Young only
Speckled sanddab	17.1	100	100
Pacific sanddab	14.0	100	97
Yellowchin sculpin	10.6	100	97
Dover sole	6.2	100	62
Stripetail rockfish	5.8	79	71
White croaker	5.3	97	32
Calico rockfish	4.8	91	24
California tonguefish	4.7	100	41
Plainfin midshipman	3.8	94	68
Halfbanded rockfish	3.4	95	38
Pink seaperch	2.9	97	79
Slender sole	2.2	62	47
English sole	1.8	100	12
Blackbelly eelpout	1.6	77	8.8
Rex sole	1.3	59	24
Roughback sculpin	1.3	82	44
Longspine combfish	1.3	94	18
Northern anchovy	1.3	47	5.9
Queenfish	1.3	68	8.8
Splitnose rockfish	1.2	50	38
Shiner perch	0.82	76	12
Hornyhead turbot	0.74	100	12
Blacktip poacher	0.65	44	12
Sportspine combfish	0.53	77	5.9
California lizardfish	0.47	65	8.8
Bigmouth sole	0.45	100	18
Longfin sanddab	0.37	77	24
White seaperch	0.32	88	18
Total Specimens	115,351		
Additional 84+ species	4,413		
Total	119,764		

*Frequency of occurrence of young fish ($\leq$55 mm SL) is given in last column.

TABLE 3

Summary of Abundance and Grequency of Occurrence of some Economically Important Fish Species* from 34 Trawl Surveys off Orange County, California 1969-1977.

Common name	Number captured	% Occurrence in surveys
Pacific sanddab	20,485	100
White croaker	6,371	97
Queenfish	1,546	68
Northern anchovy	1,566	47
California scorpion fish	312	85
Petrale sole	268	18
Chilipepper rockfish	177	38
California halibut	146	85
Cow rockfish	93	59
Pacific hake	62	32
Sabelfish	58	53
Boccacio	48	32
Lingcod	3	9

*Nearly all are young of the species.

TABLE 4

Summary of Survey Averages of Shannon-Weaver Diversity, Number-of-Species, and Number-of-Fish per Haul, for 34 Surveys off Orange County, 1969-1977: Coefficients of Variation (CV, %) Calculated for Means Among Surveys Are Compared to Average CVs from within Survey (between Sample) Variations.

	Mean/Survey ±Standard Error	Range of Survey Means	Coeffients of Variation (%)	
			Among surveys	Between samples
Shannon-Weaver Diversity/haul	1.62 ± 0.034	1.06−1.91	12.3	25.1
Number Species/haul	15.9 ± 0.51	8.6−20.8	18.5	26.3
Total-Catch/haul	469 ± 24	224−793	29.9	62
Catch-fish/haul > 55 mm SL* (n=28)	381 ± 20	164−622	27.7	NC
Catch-fish/haul $\leq$ 55 mm SL* (n=28)	104 ± 14.7	28−376	71.8	NC

*Standard Length.

periods of recruitment (May 1973, 1975, and 1977), the average was 23 species. Flatfish (mainly *Citharichthys stigmaeus, C. sordidus,* and *Microstomus pacificus*), rockfish (mainly *Sebastes saxicola, S. dalli, S. semicinctus,* and *S. diploproa*), and sculpins (mainly *Icelinus quadriseriatus*) did dominate the catches of young.

Relations to Basic Oceanographic Conditions

Visual examination of data suggested that changes in catches of young fish were related to seasonal and year-to-year changes in oceanographic conditions. To explore this in more detail, I reviewed available data on temperature and water transparency. Transparency, as measured by secchi disk depths, was chosen since other routine measurements indicative of food and productivity (i.e. plankton volumes, nutrient measurements, chlorophyll) were either not measured or not readily available for analysis. For the past five years, the trawl surveys themselves were accompanied by measurements of surface and near-bottom water temperature and by secchi disk

(transparency) readings. A brief examination of the data suggested that the largest catches occurred in cold water of low transparency. More detailed physical data was required to confirm this association, but none was available from the Orange County monitoring programs. I searched elsewhere, and found a wealth of inshore and offshore temperature and secchi disk data from 19 stations in Santa Monica Bay from weekly sampling for nearly twenty years by the staff of the Hyperion Treatment Plant. Monthly mean sea surface temperatures and secchi disk readings were calculated and plotted for the period January 1969 through April 1977 (Figures 3b and c). Regression anlysis of secchi disk data collected during the same weeks by both OCSD and Hyperion revealed a moderately good correlation ($r = 0.51, 0.1\ p < 0.05$), which improved substantially ($r = 0.7, p < .01$) when we used Hyperion values interpolated two days prior to the quarterly Orange County trawls and compared the new

sets of data. This indicated that changes in transparency at Orange County were similar to those in Santa Monica Bay and that the Hyperion records were, over the long term, representative of changes in San Pedro Bay.

Several trends were noted in the physical data. First, during the past eight years there has been a trend of increasing temperature and with notably warmer winter temperatures occurring since 1972 (Figure 3b). Secondly, only the years 1973 and 1975 showed seasonal trends that were somewhat similar; otherwise, every year appeared to have its own pattern of warming and cooling.

Variations in secchi disk readings were more interesting, however (Figure 3c). For example, the years 1969 through early 1972 were marked by relatively turbid water with only occasional periods of clear water (secchi disk depth averaged about 9 m); the spring of 1971 was particularly turbid (6 m), but clearing increased gradually into the winter of 1971-72. Beginning in 1972, three episodes of very turbid summer water (i.e. 4-5 m) followed by rapid autumn and winter clearing (to 15 m) occurred at approxiamtely 2-year intervals (fall 1972,
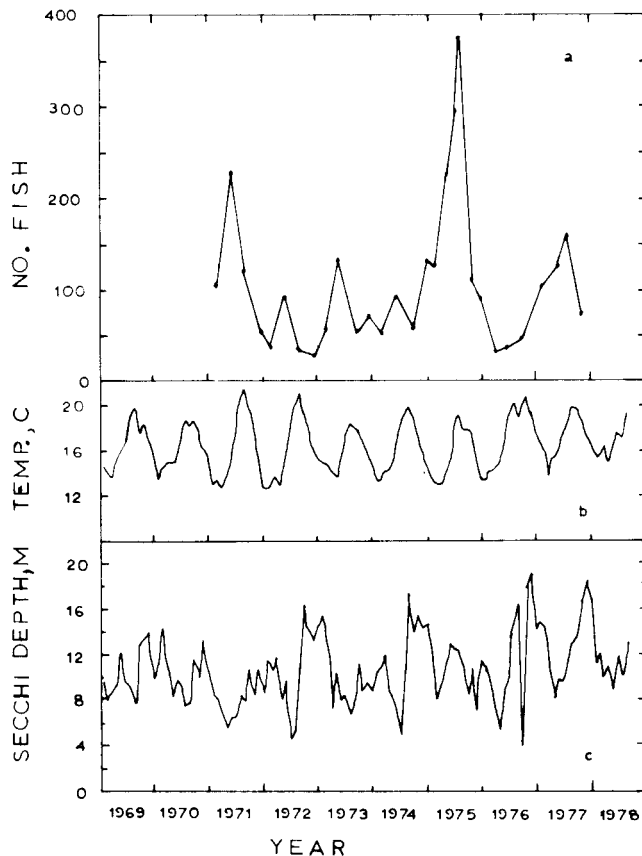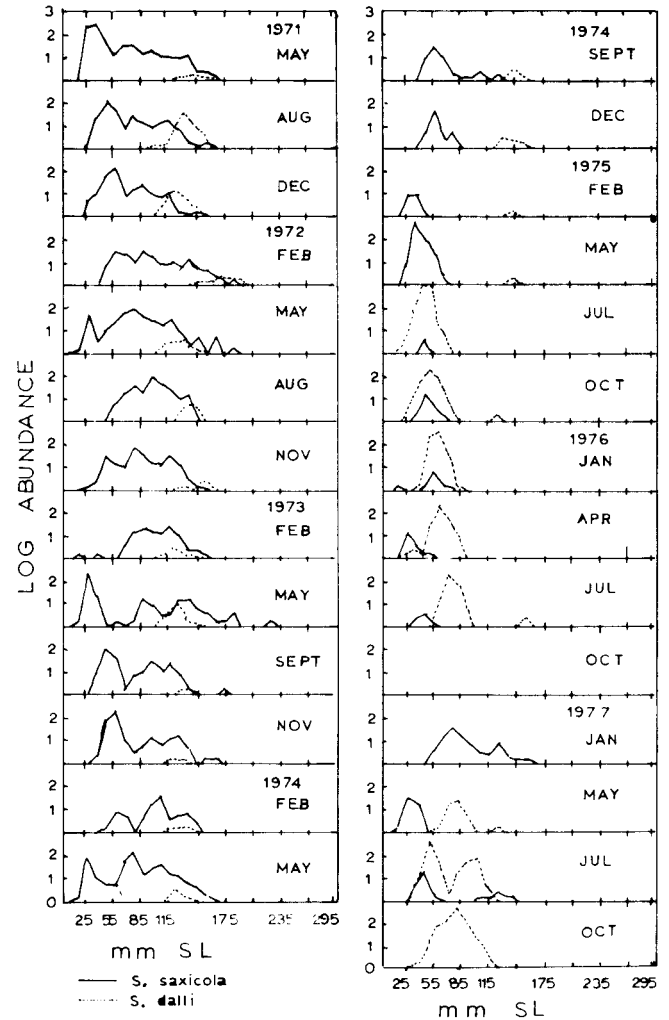

Figure 4. Length-frequency histograms for *Sebastes saxicola* and *Sebastes dalli* from 27 consecutive quarterly trawl surveys, May 1971 through October 1977. Note appearance of 25-to-35 mm standard length *S. saxicola* each spring and appearances of young *S. dalli* in the summers of 1975 and 1977. Neither species was collected in October 1976.

Figure 3. Fluctuations in (a) average catch per haul of all fish ≦55 mm standard length, (b) monthly averages of sea surface temperatures taken weekly in Santa Monica Bay and (c) monthly averages of weekly secchi disk depths from the same 19 stations.

1974, and 1976). The three episodes of very transparent water lasted approximately six months and in each case were followed by a rapid decline in transparency (winter-spring 1973, 1975, and 1977). During four of the summers (1969, 1970, 1972, and 1974), warming was accompanied by increased turbidity but not during 1971, 1973, and 1976 when summer warming was accompanied by clearing water.

Comparison of these physical events with the trawl data indicates that increasing catches of young fish were associated with episodes of cool or cooling water and decreasing clarity, whereas clear periods were generally associated with low catches. An exception during the 8-year period was the turbid-water spring of 1976, which also followed one of the warmest winters of the survey period.

There are several possible explanations for the higher catches of young fish during or just following periods of increased turbidity. The fish may be better able to see and avoid the trawl gear in clear water than in turbid water. Alternatively, the turbid water may simply be what it is— a useful indicator of high plankton activity, which includes larval and postlarval fish and their food—and thus may be marking those periods when young fish successfully arrive on the coastal shelf and when enough food exists to support their survival and growth during their first few months of life.

Juvenile Rockfish: Example of Multispecies Recruitment

In general the comparisons made above indicate that the variations in occurrence of juvenile coastal fishes is related to oceanographic episodes, which can occur at other than annual intervals. Moreover, there seem to be general patterns that are not totally obliterated by examining all species as a unit. The patterns and their relation to oceanographic conditions are applicable to recruitment of single species or species-groups and are described in the following example.

Sebastes saxicola and *S. dalli* have been the most prominent rockfish in these catches, yet they rarely occurred together in high numbers. For example, during the period 1971-75, juvenile *S. saxicola* catches averaged 41 fish/haul; in 1976 and 1977 the catches decreased 20 fold to 0.8 fish/haul. In contrast, juvenile *S. dalli* catches averaged 1.7 fish/haul during the period 1971-74, 79 fish/haul in 1975, and 55 fish/haul during the two-year period 1976-77.

Examination of length frequencies of both fish during this 7-year period revealed the patterns and events leading up to these shifts. As shown in Figure 4, both *S. saxicola* and *S. dalli* were present in the survey area in May 1971, but only *S. saxicola* was represented by recently recruited young (35-45 mm SL). This "year-class" appeared to survive and grow well during the next several years; *S. saxicola* recruited again in the spring of 1972, 1973, 1974, and 1975, again in the absence of *S. dalli*. There was also what appeared to be a progressive loss of larger "age groups" of *S. saxicola* during 1973-75. In July of 1975, the pattern established over the previous five years was obliterated when a large number of juvenile *S. dalli* invaded the survey area. This "1975" year class of *S. dalli* survived and grew (slower than *S. saxicola*). A few *S. saxicola* appeared once again in the spring of 1976. Neither species were caught in the early fall of 1976. By the next winter several age groups of *S saxicola* returned to the survey area and then J·· appeared during the remainder of 1977. Finally, in Ũ. spring of 1977 there appeared to be moderately successful recruitment of both *S. saxicola* and *S. dalli*, plus a return of older age groups of both species. In summary then, what appeared to be a stable, repeatable, and predictable pattern of recruitment of one species (*S. saxicola*) over a 4-year period was rather quickly obliterated in 1975 and resulted in a rather unpredictable alternation of species from 1975 through 1977.

One pattern was not obliterated by these changes, however. A second scan of the data in Figure 4 reveals that, whichever species was present, both contributed to strong "combined" year classes (1971, 1973, 1975, and 1977). As noted above and in Figure 3, spring conditions during these years were marked by more rapid cooling and increased turbidity than in the adjacent even-numbered years.

CONCLUSIONS

Many investigators have considered otter trawling useful in assessing the general composition of nearshore bottomfish assemblages but not useful for further quantitative or statistical assessments of bottomfish populations. In contrast, I believe the present data confirms that standardized procedures applied over a long period of time can provide insight into some of the factors that may be regulating the composition and production of nearshore fish assemblages. Certainly these data can be subjected to a more rigorous statistical analysis but in their present form do lead me to several important speculations. For example, the apparent match between recruitment episodes and physical changes suggests that oceanographic conditions are at least as important as any nearshore processes in determining the abundance of bottomfish on the mainland shelf. The patterns of the two rockfish species, moreover, suggest that once post-larval recruitment has occurred there may be important episodes of competition among the young fish. Finally, long-term sampling reaps a series of benefits as sampling continues—e.g. the first few surveys will document the principal species and something about their general abundance; several years are required to establish seasonal norms; finally, nearly all species can be encountered with 5 to 6 years of sampling, and the chance of encountering an episodic change in the major composition of the fauna increases. The effort required depends on the questions under consideration.

More detailed comparisons of these and related data on upwelling, storms, and rainfall are in progress. Meanwhile, I recommend that this or a similar survey continue so that long-term trends in nearshore fish popula- 'ions will be established for at least one site on the coast of southern California.

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LONGSHORE VARIATION IN THE DISTRIBUTION OF PLANKTON
IN THE SOUTHERN CALIFORNIA BIGHT

MICHAEL M. MULLIN
Institute of Marine Resources
University of California San Diego
La Jolla, CA 92093

ABSTRACT

The similarity of plankton samples, in terms of abundances and faunal composition, was studied as a function of distance from 100 m to 10 km by sampling with pumps from two ships simultaneously. The biomass of phytoplankton and abundances of several (but not all) zooplankters become more dissimilar the greater the separation between samples. The faunal composition changed with distance during the day but not at night.

INTRODUCTION

Knowledge of the spatial scales on which the abundance or composition of plankton changes significantly has practical importance in planning the spacing of biological oceanographic sampling stations in order to characterize a region or to detect the effects of a natural or anthropogenic perturbation (e.g. Weibe et al. 1973). It has conceptual importance in view of the intimate relation between patches or layers of abundant food and the survival and growth of zooplankton and larval fish (e.g. Mullin and Brooks 1972; Lasker 1975). In coastal waters, onshore-offshore gradients in biomass and species composition have often been observed (e.g. Eppley et al. 1977); less well known is the nature of longshore changes.

Platt et al. (1970) found that the variability in biomass of coastal phytoplankton increased as the area within which samples were taken increased to 2.6 km², and then became constant up to 10.4 km². Our original intent, stimulated by these results, was to determine whether a particularly important scale of spatial variation could be detected by departures from a simple, linear correlation between the degree of dissimilarity of two samples and their separation. Computer simulations later indicated, however, that even if patches of uniform size (but of various concentrations) had been superimposed on a "background" of uniform, low concentration, we would have been unable to distinguish the size of these patches with our sampling program.

METHODS

In March 1976, we took simultaneous samples of plankton from two ships (the R/V *David Starr Jordan* and the R/V *Townsend Cromwell*). Each pair of stations consisted of samples taken every 5 m from the surface to 35 m while the ships were separated by a known distance. This distance was varied such that spatial separations from 100 m to 10 km in longshore direction were achieved between stations both day and night. The depth of the bottom exceeded 50 m throughout the study, and the separations were chosen haphazardly over the 8 days of the cruise. From 17 through 18 March, the *Jordan* followed a cruciform drogue set at 17 m; from 19 through 25 March, the *Jordan* was at a geographically fixed station off Del Mar, California. On 24 March, sets of consecutive samples of zooplankton were taken from two fixed depths, and the records of a nearby current meter were used to determine the spacing between these samples.

Water from each depth was drawn by a diaphragm pump through a 7.5-cm diameter, plastic hose at 150 liters/minute and was collected in two 200-liter plastic tubs. After the temperature had been measured, one 50-ml aliquot was filtered through a Whatman® GF/C glass fiber filter (1-2 μm retention, the catch hereafter called "total"), and another through a Gelman® polycarbonate filter of 5 μm retention (the catch hereafter called ">5 μm"). Powdered $MgCO_3$ was added to both filters, which were then stored in 90% aqueous acetone in a refrigerator for at least 24 hours. After centrifugation, the extracted chlorophyll and phæophytin in the supernatant were determined by fluorometry (cf. Mullin and Brooks 1976). Approximately 350 liters of water collected from each depth was drained from the tubs through a flow meter into a 73 μm-meshed net, and the catch was preserved in ~5% Formalin-seawater for subsequent counting.

Hypotheses concerning vertical versus horizontal variation were tested by comparing the range of conditions to be found over all depths at any station to the range at any depth over all stations and dates.

As an index of the dissimilarity between any two simultaneous measurements at a particular depth, the absolute value of their difference divided by their sum was used. This index can range from 0 for identical data to +1 where one of the pair is zero; although the index is slightly nonlinear, it is relatively independent of the magnitude of the measurements. It is a poor index if many pairs include one zero, but this was the case only once in the data we used. The relation between this index of dissimilarity and the horizontal distance between measurements was then examined through linear regression. Note that in this analysis, the pairs of measurements of a property from each depth are treated as replicates for one scale of separation, i.e. the particular depth from which a pair was

taken is unimportant. The implicit assumption is that variation is on a similar scale at all depths sampled.

The percent similarity index (cf. Miller 1970) was also used to compare the relative proportions of different kinds of zooplankton in pairs of samples; this index is a measure of relative composition and is insensitive to absolute differences in abundance between the samples.

The samples of zooplankton were randomized and counted without knowledge of the identity of the sample. The categories of zooplankton counted, and thus contributing to the percent similarity index, were twelve developmental stages of the copepod, *Calanus pacificus*; adult *Corycaeus anglicus* (copepod); total *Evadne* (cladoceran); total *Sagitta* (chætognath); and total larvaceans. For calculating the index of dissimilarity as a function of distance, we used as one category the sum of *Calanus* naupliar stages, and the *Evadne*, *Corycaeus*, *Sagitta*, and larvacean categories. These categories were chosen to avoid many zeros and ranged typically from a few tens to several hundreds (*Calanus*, *Corycaeus*, chætognaths) or thousands (*Evadne*, larvaceans) of individuals per m^3. In samples separated by 0.1 km and ~9 km, the copepodid stages of *Acartia tonsa* were also counted.

RESULTS

The data are suitable for examining the nature of the relation between large and small phytoplankton. The simplest hypothesis is that >5 μm chlorophyll is a constant fraction of total chlorophyll; an alternative hypothesis (e.g. Malone 1971) is that large cells are particularly important when the total crop is large. In the latter case, a regression of log (>5 μm chlorophyll) on log (total chlorophyll) should have a slope of >1.0. When all data ($n = 231$) are pooled, the calculated slope is 1.02, but the 95% confidence limtis include 1.0. Hence, the simplest interpretation is that >5 μm chlorophyll is a fixed proportion of total chlorophyll, independent of crop size (in this case 47%).

Figure 1 shows the vertical distribution of temperature for each pair of stations, arranged according to increasing separation of the pair. The associated dates show the haphazard timing of pairs during the 8 days of the study. The haphazard arrangement reduces the likelihood that a unidirectional, temporal change in the area would appear to be a simple function of separation. In an ideal study, all samples would be synoptic.

Profiles of temperature varied somewhat between stations but were sufficiently similar that median range of temperature at each depth was less than the median range over 35 m at each station ($p = 0.013$ for one-tailed, rank sum test on ranges). This means, unsurprisingly, that the vertical variation in temperature exceeded that horizontally and temporally.

The same tendency was true for cholorophyll; the hori-

zontal and temporal variation (as measured by the range) at a depth was less than the variation in the upper 35 m of the typical station. However, the difference was not statistically significant ($p = 0.08$ for one-tailed rank sum test on ranges). Thus, a population of zooplankton distributed vertically throughout the upper 35 m would typically experience at least as wide a range of conditions at a single station as would a population confined to a single depth throughout the study.

Similarity in temperature is one indication of physical similarity between stations. The indices of dissimilarity for temperatures measured 0.1 km apart were no less than
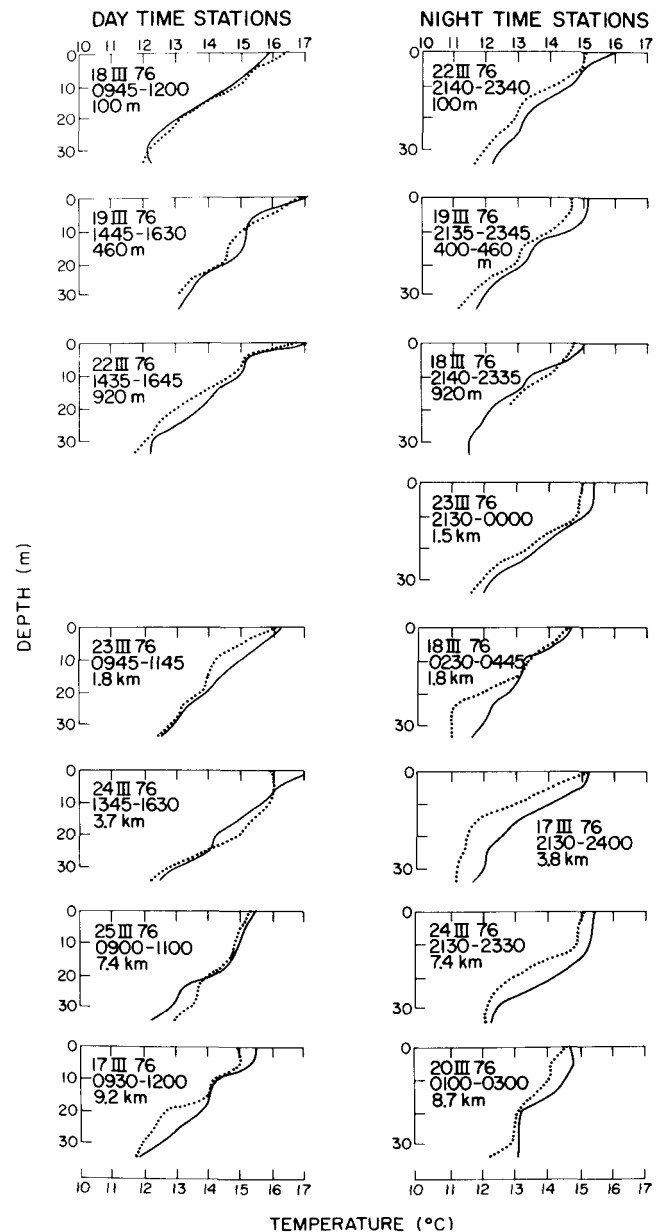

Figure 1. Profiles of temperature measured simultaneously on the R/V *David Starr Jordan* (solid line) and R/V *Townsend Cromwell* (dotted line) separated by different distances.

the indices for measurements 8.7 and 9.2 km apart ($p =$ 0.34 for one-tailed, rank sum test). Further, there was no significant correlation between index and distance in the complete set of data ($r = 0.1$ for $n = 115$, $p > 0.1$ of no correlation). The stations farthest apart were thus as similar, in terms of temperature, as the stations nearest to each other.

This was not the case for either total or >5 μm chlorophyll; the concentrations measured 0.1 km apart were less different than those measured 8.7 and 9.2 km apart, and there was a significant, positive correlation between index of dissimilarity and spatial separation ($p < 0.05$ for all 4 tests). Thus, concentrations of chlorophyll at a given depth at stations far apart were generally more dissimilar than those at stations close together (Figure 2). This trend obviously has an upper limit at some distance, since concentrations never become infinitely large or small. Relations other than a linear one between distance and dissimilarity in chlorophyll were tested; in some cases these accounted for more variability than did the linear relation, but the improvement was not statistically significant by F test.

The abundances of *Corycaeus* and the larvaceans did not become more variable with distance (i.e. no significant correlation between dissimilarity and separation), but the variability in *Calanus* nauplii, *Evadne*, and *Sagitta* increased ($p < 0.05$ of no correlation for $n = 97$). As noted above, this trend must have an upper limit at some greater distance. The relations for *Calanus* and *Evadne* are shown in Figure 3.

This result would be obtained if *Corycaeus* and the larvaceans were much less variable at all distances sampled than were the other three categories. However, the indices of dissimilarity refute this explanation; these indices for the larvaceans at 0.1 and 1.0 km separation are less than the comparable indices for *Calanus*, *Evadne*, and *Sagitta*, but the indices for *Corycaeus* are greater.

It therefore seems that the predominant scales of variability fall into three groups: 1) The larvaceans were relatively homogeneous in distribution at all scales sampled; 2) *Calanus*, *Evadne*, and *Sagitta* became more variable with increasing distance; and 3) *Corycaeus* was relatively variable even in closely spaced samples. There is no obvious, biological reason for this; the two carnivores (*Sagitta*, *Corycaeus*), the two most narrowly defined categories (*Calanus*, *Corycaeus*), the two must abundant categories (*Evadne*, larvaceans), and the two categories with the most consistent gradient in abundance with depth (*Evadne* and larvaceans, both of which were usually much more abundant in the upper 10 m than at 30-35 m) all split into different groups.

The percent similarity index, which is based on the relative abundances of the 16 counted categories (i.e. each developmental stage of *Calanus* treated as a dis-
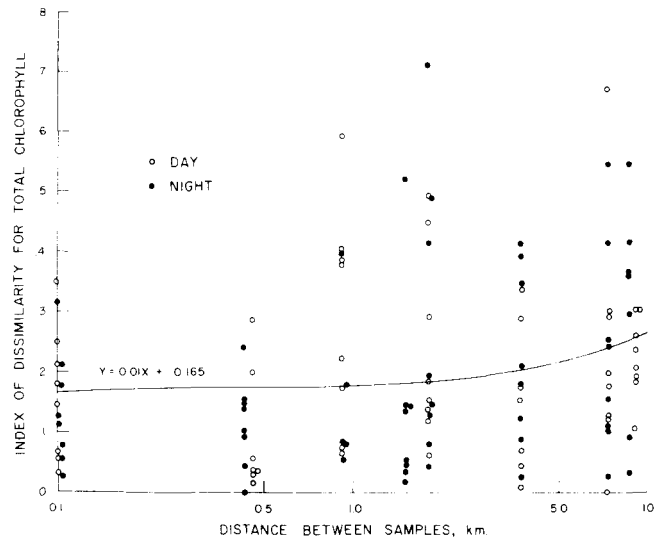

Figure 2. Index of dissimilarity ($|A-B|$ / ($A+B$)) as a function of distance. The linear relation appears curved on the semi-logarithmic plot.

tinct entity) decreased from 82% for the nearest samples to 68% for the farthest (Figure 3). Even at almost 10 km, however, some samples were very similar (index $> 85\%$).

It is not surprising that samples taken far apart are less similar in composition than those taken close together. When day and night are treated separately, however, an interesting aspect emerges. The samples taken at night show no decrease in percent similarity with increasing separation ($p > 0.1$ of no correlation), while samples taken during the day are increasingly similar as they are closer together ($p < 0.01$ of no correlation). For the daytime samples alone, the linear regression equation is $Y = -1.97X + 82.7$, where X is separation in km and Y is percent similarity index. The slopes of the linear regressions for daytime and nighttime data are significantly different. Recalculation of percent similarity indices to include available data on *Acartia* copepopdites indicates that the pattern is maintained in spite of this addition.

This finding is interestingly, though probably coincidentally, like that of Miller (1970), who studied change in percent similarity index over time while following a "migrating" drogue. Miller's results indicated that the decrease in similarity with time at 100 m occurred primarily during the daylight hours; the temporal decay in similarity appeared to be suspended at night.

DISCUSSION

We do not know how general these results will prove to be, in terms of applicability to other seasons or other coasts. Based on our results, simultaneous samples from specific depths within one or two kilometers of each other in a longshore direction are likely to be as similar as samples spaced more closely; at greater separation, samples are increasingly likely to be dissimilar in abundance
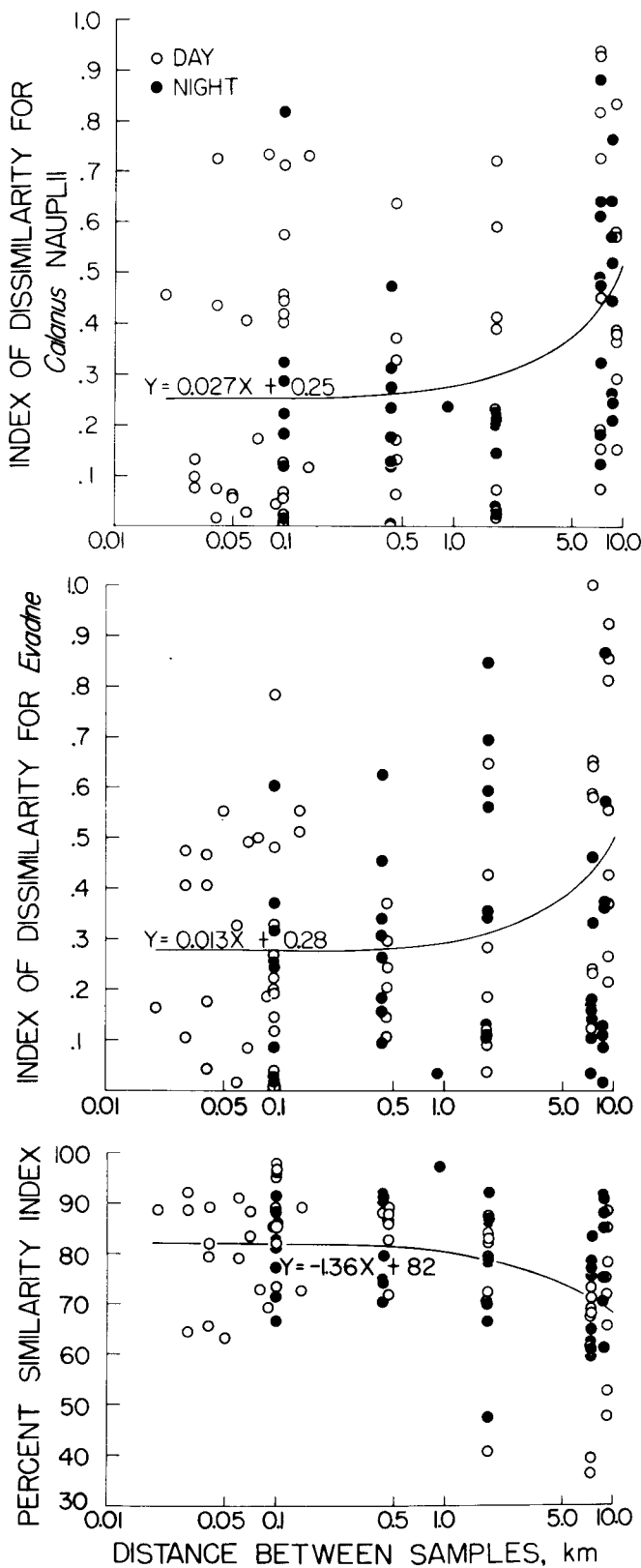
Figure 3. Upper—Index of dissimilarity for *Calanus* nauplii as a function of distance; Middle—Index of dissimilarity for *Evadne* as a function of distance; Lower—Percent similarity of zooplankton as a function of distance. In all, the linear relation appears curved on the semi-logarithmic plot.

of some species and in relative composition. Location of "replicate" or "control" stations for plankton sampling should be adjusted accordingly, depending upon the degree of similarity that the investigator requires (or the dissimilarity that is to be detected) and the inevitable limitations of time and funding.

The finding that the faunal composition of widely spaced samples is more similar at night than by day, if it proves to be general, raises the possibility that an anthropogenic change in composition might be more easily detected at night, since the unperturbed composition would be similar over a large area.

The biological causes of this finding are not clear. Migration into the surface layers of abundant, homogeneously distributed forms that therefore dominate the percent similarity index at night could give this result, but except for the rare copopodite stage V and adult *Calanus*, which were most abundant at night, the categories we counted were similar in abundance night and day. This also suggests that predation on the zooplankton was not markedly higher at night than by day.

The result could also be obtained if the zooplankters dispersed horizontally and vertically during the night and were more aggregated by day; were this the case, the variance in abundance of each category should be significantly greater by day than at night. This was true ($p < 0.05$ by F test) for some categories, notably *Sagitta* and the youngest naupliar *Calanus*, but not true for larvaceans and the early copepodite stages of *Calanus*. The most abundant category (*Evadne*) was more variable during the day, but the significance was questionable ($p \sim 0.05$). *Corycaeus* was significantly more variable at night. The overall evidence is therefore equivocal.

Another explanation—one which seems less biologically plausible than those already examined—is that although the zooplankters are equally patchy day and night, patches of all categories tend to overlap much more at night than by day. Thus, the relative composition of samples taken at night tends toward constancy because the abundances of categories vary together horizontally. One can imagine several hydrodynamic or biological causes of such covariance; it is less easy to explain why this agreement should break down each day. Tending to refute this hypothesis (in addition to its implausibility) is the finding of Smith et al. (1976) that longshore patches of nearshore zooplankton off Oregon during the daytime tended to be multispecies entities.

ACKNOWLEDGMENTS

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MICROPLANKTON AND OTHER SESTON COMPONENTS IN COASTAL WATERS NEAR THE POINT LOMA (SAN DIEGO) SEWAGE OUTFALL

J.R. BEERS, F.M.H. REID AND G.L. STEWART
Institute of Marine Resources
University of California San Diego
La Jolla, CA 92093

ABSTRACT

A report of high phytoplankton abundance at the Point Loma (San Diego) sewage outfall in July 1970, presumably as the result of increased nutrient supply, prompted our study on two occasions (June 1972 and August 1973) of a series of sites extending approximately 8 km to both the north and south of the outfall in an attempt to detect any enhanced activity of the larger microplankton (mainly dinoflagellates, which could be heterotrophs, and microzooplankton) near the outfall. Standing stocks of nutrients, seston dry weight, adenosine triphosphate (ATP), chlorophyll a, and microplankton taxa and abundance (principally in the 35-μm mesh net fraction) were determined over the water column. A plume of ammonia, most pronounced at approximately 30-40 m, was found in June 1972 extending from the outfall to the north and northwest. At the stations north of the outfall, both the seston dry weight and ATP levels were higher in the depth interval coinciding with the enhanced ammonia levels than they were at the southern stations. The components of the microplankton studied did not show marked differences in abundance.

INTRODUCTION

Numerous coastal municipalities, including San Diego, continually discharge effluent from sewage treatment plants into the nearshore marine environment. Chemical substances in the discharges include material that may be utilized by heterotrophic and autotrophic organisms for their growth and reproduction. For example, the abundant ammonia that has been found in the effluents (Thomas 1972; Hendricks and Harding 1974) could provide an important nitrogen source for photosynthetic forms. If the magnitude of the input of nutrients from the outfalls relative to the level supplied from other sources, e.g. in situ regeneration and upwelling, is large, then it can be hypothesized that the regions around such effluents have the potential for supporting relatively high production which may be seen as large standing crops of organisms. Realizing this, however, would be dependent upon such factors as the nature of the circulation in the affected area; the absence of growth-suppressing materials such as heavy metals, organic pesticides, etc. in the discharge; and zooplankton grazing pressures that do not result in rapid cropping of new production. Nutrient and hydrographic studies of San Diego coastal waters (e.g. University of

California, Institute of Marine Resources 1968), while showing periods of intense upwelling with relatively high nutrient levels within the euphotic zone, also show extensive periods when nutrient values are low and probably limiting to primary production. It is during these latter periods that outfall discharges would be most apt to have a demonstrable effect on populations of autotrophs.

Interest in the effects of outfall discharges into southern California waters on planktonic and benthonic populations is relatively long-standing (e.g. Resig 1959, 1960; Allan Hancock Foundation, University of Southern California 1965a, b). In more recent years there has been quickened concern with outfall areas due to the fear that discharges into the marine environment might be detrimental to the varied uses of coastal waters. The opportunities for observations on factors affecting biological production provided by the outfall sites stimulated studies of the plankton near southern California outfalls, including that at San Diego (i.e. the Point Loma outfall), by several members of the University of California's Institute of Marine Resources (e.g. University of California, Institute of Marine Resources 1972; Eppley et al. 1972; Thomas 1972). These studies considered primarily the photosynthetic populations within the euphotic zone and provided evidence that the areas directly adjacent to outfalls, including that at Point Loma, can be, at least at times, eutrophic compared to other coastal regions. Eppley et al. (1972) reported eutrophication at the San Diego outfall, evidenced by phytoplankton crops and productivity several times higher than that at a "control" site near the Scripps Canyon off La Jolla. In addition, their calculation of specific growth rates for the phytoplankton crop at the outfall showed similar rates to those at the control site, thus implying no strong inhibitory effects of the discharge.

The role of trophic levels above that of primary producers within the euphotic zone at the outfalls has received relatively little attention. The purpose of the present study was to identify and quantitatively describe the animal as well as the plant components of the microplankton populations (i.e. pelagic organisms other than bacteria that would normally pass approximately 200-μm mesh netting) directly at the San Diego outfall and at adjacent sites that would not be expected to have significant chemical enrichment from the sewage discharge. The work concentrated on the fraction of the micro-

plankton that would be retained on 35-μm mesh netting. Amongst the dominant components of this population are the dinoflagellates, many species of which may be heterotrophic or even phagotrophic. Also prominent are ciliate protozoans which, because of their mode of reproduction and reproductive capacity, are in a position to affect food chain dynamics in a markedly different manner from metazoans. Most importantly, they have the ability to respond quickly to changes in their environment, and species successions can occur rapidly. The predominant micrometazoans are copepod developmental stages.

In contrast to some earlier studies, the total water column, to within a few meters of the bottom, was examined. If the populations resulting from higher primary production in the euphotic zone were not being utilized or removed by lateral transport, they could be settling and providing the basis for enhanced heterotrophic and/or phagotrophic activity below the compensation depth. Organic enrichment from the outfall could be utilized for heterotrophic production. Hence, when the discharge wastefield is effectively held below the euphotic zone by its density characteristics relative to the upper water, the potential for heterotrophic/phagotrophic production at some deeper level of the water column may be established.

In addition to microscope study of the microplankton, chemical or gravimetric estimates were made of other parameters of the microseston. The nutrient concentrations and hydrographic conditions were examined at each station.

MATERIALS AND METHODS

Sampling was done from the R/V *Alexander Agassiz* at 10 sites within a grid extending 5 miles (8.1 km) to the NNW and SSE and 1.5 miles (2.4 km) seaward of the outfall (Figure 1) during the daylight hours of 23 and 24 June 1972. Stations 1-7 were repeated during the day of 10 August 1973. Stations 1-7 were in an approximately straight line following the contour of the water depth found at the outfall. Except for the two southerly sites off the mouth of San Diego Bay, the stations were approximately equidistant from shore. The numbering of the stations is in the order of sampling in June 1972. In August 1973 the stations were sampled from south to north, i.e. 7, 6, 5, 1, 2, 3, and 4.

Some earlier studies of the outfall plankton populations have employed control stations at greater distance from the outfall than our most distant site and often with different characteristics such as water column depth, euphotic depth, distance from shore, etc. (e.g. Eppley et al. 1972 used the Scripps Canyon off La Jolla). Studies of the benthic populations in the vicinity of Point Loma have indicated an assymetrical gradient of effects around the outfall. Chen et al. (1972 seen in Southern California Coastal Water Research Project [SCCWRP] 1973) found
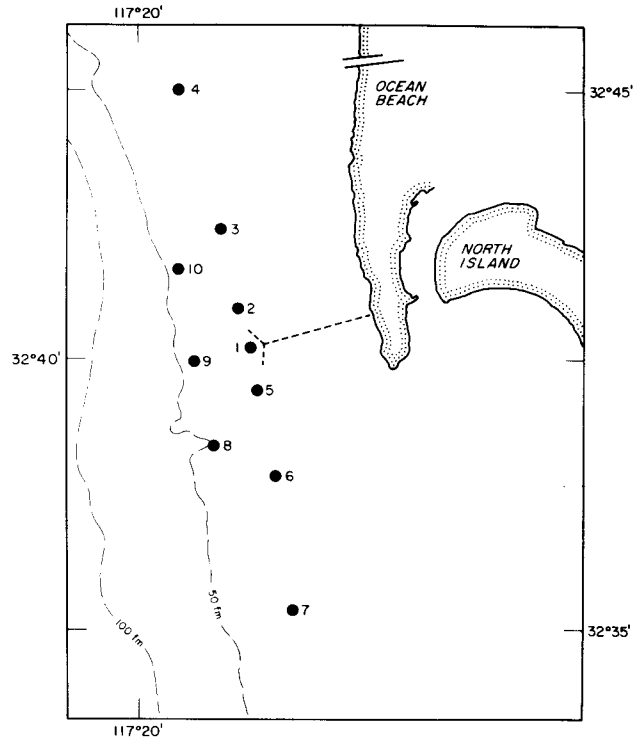
Figure 1. Location of sampling sites. Station 1 is at the terminus of the outfall.

that stations to the north show a more marked effect than those to the south. In this study we have chosen to examine a series of similarly situated stations to both the north and south of the outfall, presuming that, dependent upon the circulation at the time of the observations, one direction would be downstream of the discharge whereas the other would be upstream. Considering the total water column, however, this can be complicated if the currents vary at different depths. Hendricks (SCCWRP 1973), in his modelling of the phytoplankton in outfall areas, points out that maximum response could occur at some distance (e.g. several km) from the discharge. Dependent upon the amount of shear, if any, between surface and subsurface currents, the discharge may be moving in one direction away from the outfall while enhanced phytoplankton crops could appear in the opposite direction.

A pumping system, incorporating a Flotec Inc. Rotalator Impeller Pump (Series R5S1), 1-inch (2.5-cm) I.D. Heliflex™ reinforced PVC hose, a voluming meter, and plankton concentrator (35-μm mesh netting), was used to obtain integrated samples over four standard depth intervals of surface–15 m, 15–30 m, 30–45 m, and 45 to within a meter or two of the bottom (60–70 m) at each station. The hose intake was moved through the water column at appproximately 1.5 m/minute.

A constant fraction of the pumped water was accumulated over each depth interval for analysis of chlorophyll *a* and phæophytin by the fluorometric method (Yentsch

and Menzel 1963; Holm-Hansen et al. 1965), adenosine triphosphate (Holm-Hansen and Booth 1966), and total seston dry weight by a modification of the procedure of Banse et al. (1963) in which an ammonium formate solution, isotonic with seawater, was used to rinse the filters of salts. Sample volumes varied depending upon their content of total particulate matter. In June 1972 they averaged 500 ml for chlorophyll a, 376 ml for ATP, and 942 ml for seston dry weight; and in August 1973, 331 ml for chlorophyll a, 341 ml for ATP, and 549 ml for seston dry weight. The chlorophyll filters from the June 1972 sampling were inadvertently removed from the freezer for an unknown length of time, possibly as long as 48 hours, but were *not* exposed to light. Tests simulating the various possible conditions of this occurrence using water with the same approximate chlorophyll level indicated that a consistent loss of up to approximately ¼-⅓ of the chlorophyll could have resulted. Hence, the data are used only in supplementary discussion.

The pumped water also provided an unconcentrated (UNCONC) sample of the small microplankton for determination of the numerical abundance and biomass of taxa too small to be quantitatively retained on 35-μm mesh netting. These samples have been enumerated at selected sites only. The larger components of the microplankton were concentrated on 35-μm mesh netting (+35 CONC samples) from approximately 60-150 liters of pumped seawater. Fixation/preservation of both the UNCONC and +35 CONC samples was at 2% formaldehyde. Sodium borate and SrCl₂ were included in the fixative to aid in the preservation of calcareous and strontium-containing organisms, respectively. Analysis of the samples was by inverted microscope procedures described in Reid et al. (1970) and Beers and Stewart (1970).

Taxa identified in the +35 CONC samples were those that would be expected to be quantitatively retained on 35-μm mesh netting and that could be identified at magnifications of 100-200X. Non-thecate dinoflagellates were not included because of possible damage to these delicate forms during net concentration. In general, one subsample of the greatest volume that could be settled without being too dense for good counting was studied from each sample. The unconcentrated sample volume represented in each +35 CONC subsample varied but was generally at least a liter.

In the Results section that follows, the measure of variability routinely given is one standard deviation. When stations to the north and south of the outfall are compared and there is no overlap of a parameter's mean ± one standard deviation they will be considered "dissimilar." They will be identified as "different" if there is no overlap of the means ± two standard deviations. In addition, a non-parametric statistic, the Mann-Whitney rank test (see Tate and Clelland 1957), having no assump-

tions as to the normalcy of the data, was used to detect differences between stations. Because of the limited number of sites being compared, the test provides an indication of difference only to the 0.10-probability level.

In order to characterize the environment of the microplankton, hydrographic (temperature and salinity) and nutrient chemistry measures (nitrate and nitrite-N, ammonia-N, and phosphate-P by methods outlined in Strickland and Parsons 1972) were made on Nansen reversing water bottle samples from every 10 m (surface to 60 or 70 m) over the total water column depth.

RESULTS

Hydrography

Temperature profiles for the two studies are shown in Figure 2. Average surface temperature was 20.1 (±0.3)°C in June 1972 and 18.6 (±0.2)°C in August 1973. At 10 m, average levels were: June 1972, 15.8 (±2.1)°C; August 1973, 13.1 (±1.0)°C. The relatively large standard deviation of the June 1972 data results mainly from Station 2 where the upper 10 m appeared to be isothermal. The average drop in the upper 10 m was 4.2°C ($\Delta\delta_t$, − 0.9) in June 1972 and 5.5°C ($\Delta\delta_t$, − 1.2) in August 1973. Expendable bathythermograph casts taken at selected stations in August 1973 showed the drop could be over a relatively few meters, with the temperatures in the upper part of the depth interval being approximately uniform. A further temperature decrease in the depth interval from 10-20 m averaged 2.9 (±1.6)°C ($\Delta\delta_t$, − 0.6) in June 1972 and 1.5 (±0.9)°C ($\Delta\delta_t$, − 0.3) in August 1973. Decreases in deeper intervals of the water column were relatively small.

Direct measurement of submarine light conditions was not made, but Secchi disc lowerings were done at a few stations on each cruise. Readings ranged from approximately 3.5–5 m, suggesting the photosynthetic compensation depth may have been no deeper than about 15 m (i.e. 3X Secchi depth).

Nutrient Chemistry

Inorganic nitrogen (ammonia-N and nitrate + nitrite-N) and phosphorus concentrations were determined at all stations in June 1972, but only ammonia, as a tracer of the outfall effluent, was quantified for the August 1973 samples. A plume with high concentrations of ammonia (maximum, 6.2 μg-atoms NH₃−N/l at 40 m, Station 1) originating at the outfall and extending to the north and northwest (Station 10, 1.39 μg-atoms NH₃−N/l at 40 m) was seen in June 1972 (Figure 3). The August 1973 samples showed no similarly enhanced levels of ammonia
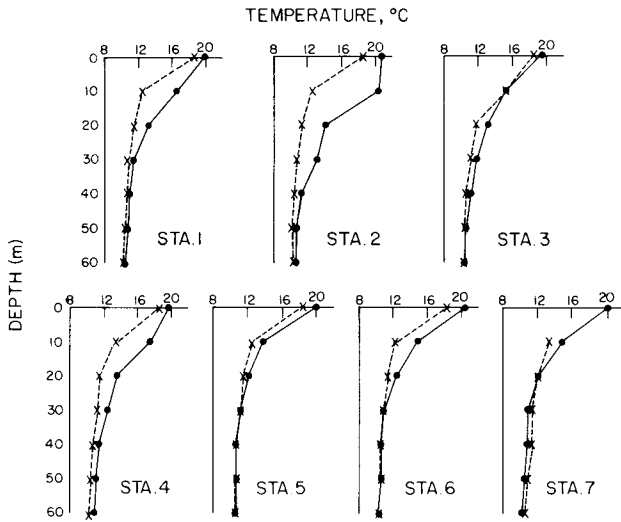
TEMPERATURE, °C

Figure 2. Temperature profiles. ● = June 1972; x = August 1973.

AMMONIA-N, μg A / l
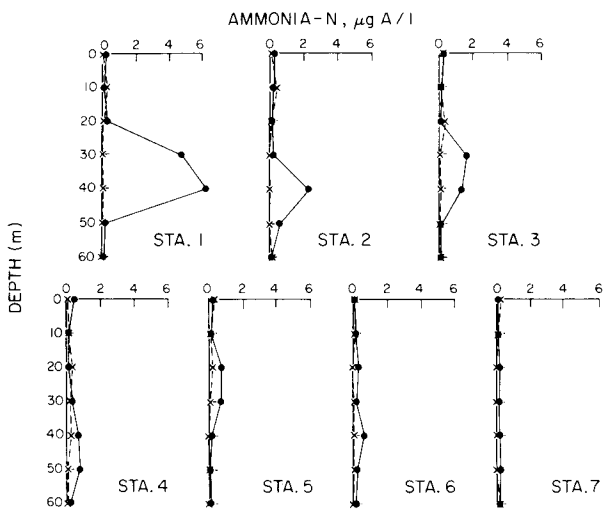
Figure 3. The vertical distribution of ammonia-nitrogen. ● = June 1972; x = August 1973.

to either the north or the south (Figure 3).

Levels of nitrate + nitrite-N (June 1972) were often undetectable or at concentrations less than 0.2 μg-atoms/ liter in the surface down through the 20-m samples at the outfall and sites to the north, whereas the 20-m samples at stations to the south were within the nitrocline (Stations 5-7, 20 m; average 3.72 μg-atoms NO₃ + NO₂ − N/liter). Phosphate, alhtough often low in the upper waters, was generally present at detectable levels (Stations 1-7, surface: 0.07±0.05μg-atoms PO₄−P/liter; 10 m: 0.17±0.7 μg-atoms PO₄−P/liter). As seen in the nitrate + nitrite-N
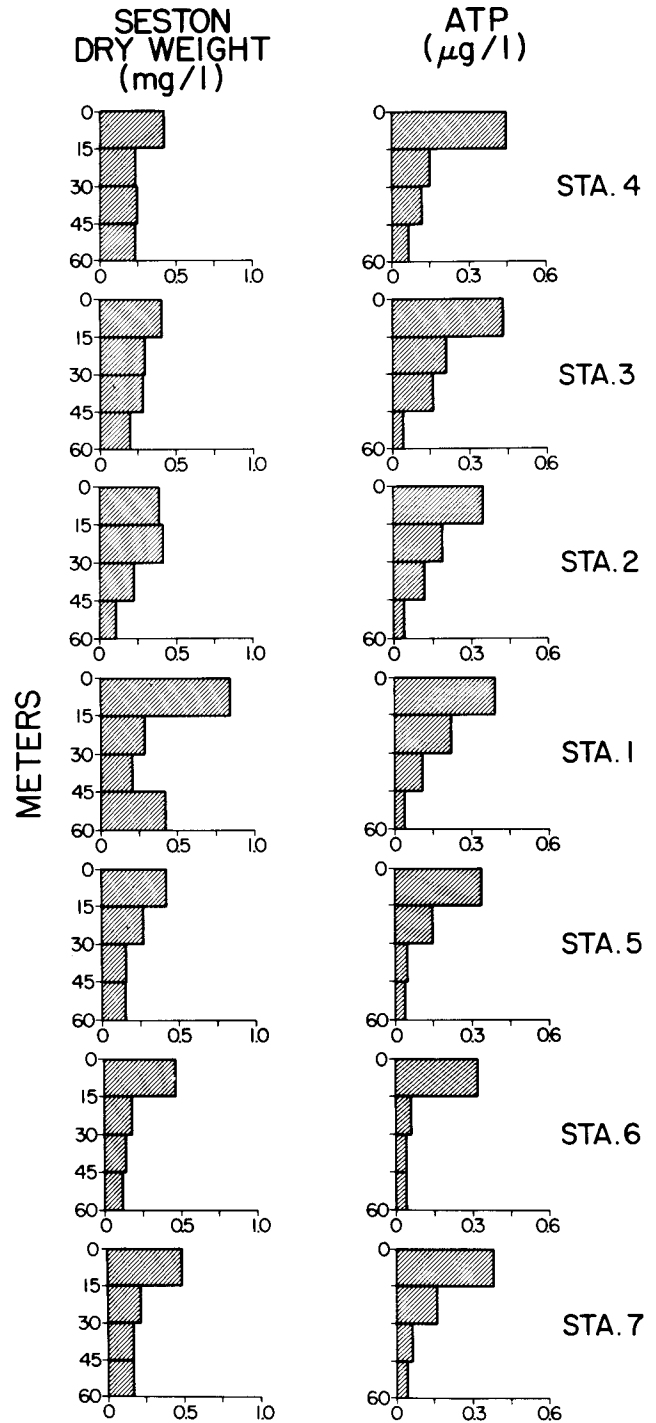
Figure 4. Seston dry weight and ATP abundance; June 1972 (stations are given, top to bottom, as they occur north to south).

data, at 20 m the southern stations (Stations 5-7) had comparably higher phosphate (0.77 ±0.18 μg-atoms PO₄− P/liter) than those (Stations 2-4) to the north (0.30 ±0.10 μg-atoms PO₄−P/liter).
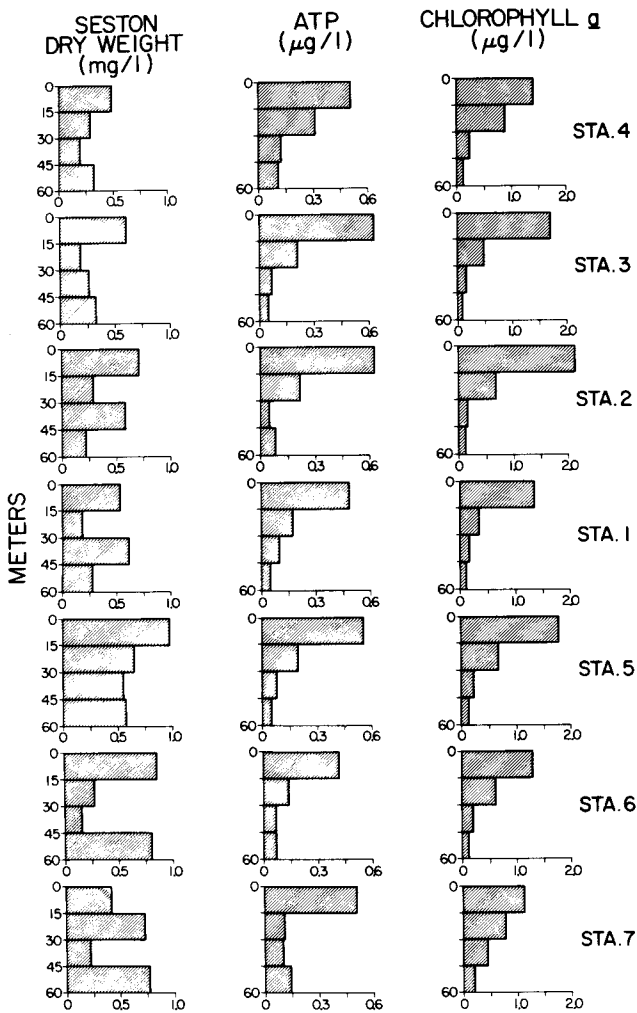
Figure 5. Seston dry weight, ATP, and chlorophyll a abundance; August 1973 (stations are given, top to bottom, as they occur north to south).

Measures of Seston Components

Depth profiles of the total seston dry weight, chlorophyll a, and ATP at Stations 1-7 are shown in Figures 4 and 5 for the June 1972 and August 1973 studies, respectively. Values integrated over the water column are given in Table 1.

The dry weight of the seston provides a measure of the total combined living and detrital materials. In June 1972 the greatest average abundance of seston over the whole water column was found at the outfall site, primarily the result of levels approximately twice the average for all stations in the 0-15 m and 45-60 m depth intervals. Although the outfall discharge is of dissolved and not suspended (sludge) materials (personal communication), its flow could result in some disturbance of the sediments. Stations to the north of the outfall showed slightly higher average levels (0-60 m, 286 ±8 μg dry weight seston/liter) than those to the south (0-60 m, 249 ±19 μg/liter). Seston abundance within the various depth inter-

TABLE 1

Average Levels[1] of Microseston Dry Weight, Adenosine Triphosphate, and Chlorophyll a over the 60 m Water Columns of Stations 1-7.

	23-24 June 1972			10 August 1973		
Station	Micro-seston	Chl a^2	ATP	Micro-seston	Chl a	ATP
1	440	0.25	0.19	410	0.49	0.20
2	280	0.28	0.18	450	0.77	0.25
3	300	0.26	0.21	350	0.61	0.24
4	280	0.27	0.20	330	0.67	0.27
5	250	0.25	0.15	700	0.71	0.22
6	230	0.18	0.12	530	0.54	0.18
7	270	0.21	0.16	540	0.63	0.22

1. in μg/liter
2. see under Materials and Methods

vals at the stations to the north and south was similar (i.e. within ± one standard deviation) except for 30-45 m, where the plume of ammonia was observed. Stations to the north were uniformly higher (247 ±31 μg dry weight seston/liter) than those to the south (157 ±15 μg/liter). The difference was also shown by the Mann-Whitney rank test. In August 1973 a difference in total seston within the bottom depth interval (45-60 m) was seen, with stations to the south being higher (723 ±122 μg dry weight seston/liter) than those to the north (294 ±91 μg/liter).

ATP provides an index of the abundance of all living organisms including autotrophs, heterotrophs, and phagotrophs in the seston (Holm-Hansen and Booth 1966). Its distribution pattern during the June 1972 study was similar to that determined for the total seston dry weight, which also includes detritus. The average ATP level over the 60-m water column was lower at southern stations (0.14 ±0.02 μg/liter) than northern stations (0.20 ±0.02 μg/liter), principally because of the 30-45 m depth interval in which ATP levels to the north were approximately twice as high (Stations 2-4, 0.13 ±0.02 μg/liter) as those to the south (Stations 5-7, 0.05 ±0.01 μg/liter). This interval includes the depths at which the ammonia plume originating from the outfall was detected. In August 1973 no differences were observed between stations in either direction from the outfall, including the 45-60 m depth interval in which high abundance of total seston was found south of the outfall.

Chlorophyll a provides an index of the phytoplankton standing crop. Reliable determinations are available only from the August 1973 cruise. No differences for any depth interval were seen between stations situated to the north or south of the outfall. The average level for the upper 15 m of the 7 stations was 1.50 (±0.35) μg chl a/liter, dropping to 0.64 (±0.18) μg chl a/liter at 15-30 m. In June 1972 the average chlorophyl a levels determined from Stations 1-7 were: 0-15 m, 0.45 (±0.07) μg/liter and 15-30 m, 0.31 (±0.10)μg/liter. Although the absolute levels are probably low by ¼ to ⅓ because of the

accidental thawing of the filters, our examination of the effects of the thawing suggests that any relative differences would be retained. Similar to the August 1973 results, stations to the north and south of the outfall were not different at any depth.

The Microplankton

Total Population

Total microplankton was studied at the outfall (Station 1) and the extreme northern site (Station 4). In addition, samples from the most southern location (Station 7) were studied in August 1973. The station at the outfall was chosen for comparison with the more distant sites since the evidence of eutrophication reported by Eppley et al. (1972) was directly over the outfall.

The organic carbon content of the microplankton, subdivided into major taxonomic groups, is given in Table 2. Marked differences in the average microplankton carbon over the total water column were not seen between stations on either cruise. In June 1972 average carbon abundance (0-60 m) was slightly more than 20 μg/liter. Levels at the same depth interval but at different stations did not differ markedly. In August 1973 microplankton carbon was only about half as high in the upper 15 m at Station 7 as it was at Stations 1 and 4. However, levels in the other depth intervals were generally 2-4 times higher at Station 7, so averaged over the entire water column values were similar: Station 1, 31.8 μg C/liter, Station 4, 36.5 μg C/liter; and Station 7, 25.9 μg C/liter. The differences at Station 7 relative to the other two sites do not result from any one taxon but are general over most of the major groups. Of the total microplankton carbon, animal components accounted for <10% in the upper interval, increasing with depth to approximately 25%.

The diatom (i.e. pennate and centric) carbon in the depth interval of the ammonia plume at the outfall site in June 1972 was only ¼ that at the same depth of Station 4, and at 15-30 m it was only slightly greater than 50% of that seen at the site away from the outfall. The magnitude of these differences was as large or larger than any others seen between stations for all taxonomic groups on this cruise (but not larger than many seen in August 1973). It can be tentatively suggested that this may have resulted as an effect of the outfall discharge.

The factor, 286 × ATP concentration has been suggested as providing an estimate of the carbon content of the total living matter (Holm-Hansen 1973). Using this calculation and comparing it with the carbon abundance of microplankton determined from direct microscopy, it can be seen that it is in the upper depth interval that the organisms in the microplankton size range make their greatest contribution to the total biomass and that the fraction for which they account decreases with depth. The ratio of microplankton carbon, determined from microscopy, to ATP averaged 176:1 (range 108-233:1)

TABLE 2
Organic Carbon Content* of the Major Taxonomic Groups of the Microplankton.

	Pennate diatoms	Centric diatoms	Thecate dinofla-gellates	Non-thecate dinofla-gellates	Cocco-litho-phorids	"Monads and fla-gellates"	Pro-tozoa	Micro-metazoa
23-24 June 1972								
Station 1								
Surf-15m	0.30	0.43	15.	4.3	20.	13.	1.8	2.5
15-30m	0.54	0.37	1.9	0.90	5.7	4.6	0.77	2.9
30-45m	0.21	0.15	0.61	0.75	1.8	1.6	0.41	1.2
45-60m	0.15	0.12	0.34	0.55	0.56	1.3	0.47	0.37
Station 4								
Surf-15m	0.45	0.47	13.	5.1	19.	13.	1.1	2.3
15-30m	0.93	0.69	1.7	1.5	4.6	7.7	0.49	2.0
30-45m	0.59	0.86	0.84	0.87	2.6	2.3	0.64	1.7
45-60m	0.21	0.10	0.58	0.86	0.38	1.0	0.24	0.71
10 August 1973								
Station 1								
Surf-15m	1.8	2.9	4.7	20.	13.	69.	3.6	2.9
15-30m	0.12	0.92	0.31	2.5	1.4	3.3	0.72	1.9
30-45m	0.14	0.30	0.09	0.93	0.27	1.4	0.30	0.84
45-60m	0.06	0.26	0.70	0.60	0.50	2.0	0.34	0.54
Station 4								
Surf-15m	2.5	2.3	6.5	16.	10.	81.	4.0	3.5
15-30m	0.55	0.95	0.72	1.6	3.7	8.0	1.7	3.4
30-45m	0.39	0.48	0.48	0.87	1.0	4.2	0.59	2.0
45-60m	0.14	0.35	0.08	0.90	0.61	2.1	0.30	0.51
Station 7								
Surf-15m	0.68	1.1	6.2	5.1	5.9	36.	ND†	1.9
15-30m	0.23	2.5	2.2	4.4	7.7	15.	ND	2.3
30-45m	0.13	0.68	0.53	1.6	1.1	7.0	ND	1.8
45-60m	0.21	0.21	0.16	2.3	0.26	2.6	ND	0.7

* in μg C/liter
† not determined.

for the 0-15 m depth interval at the five stations where total microplankton was studied on the two cruises. This dropped with depth to 64:1 (range 38-98:1) for the 45-60 m depth interval. If the calculation is valid, and assuming the remaining "living" carbon is bacterial, populations of such microbes would comprise fractions of the total microplankton biomass ranging from approximately 38% (0-15 m) to almost 80% (45-60 m).

+35 CONC Phytoplankton Taxa

Thecate dinoflagellates generally dominated the +35 CONC phytoplankton in both numbers and biomass. It is probable that an important fraction of these may be heterotrophic, at least at times, but their identification as such is not possible from our preserved samples. The Mann-Whitney rank test indicated some differences in populations of the large dinoflagellates between stations north and south of the outfall. In June 1972 there was evidence of both relatively high numbers and carbon in the 15-30 m depth interval north of the outfall and of high numbers, but not carbon, at 30-45 m. The ammonia plume and high levels of other seston components were seen in the latter depth interval. For the August 1973 samples, the rank test indicated that stations to the south

had greater numbers of thecate dinoflagellates and that carbon was higher in all depth intervals below the upper one. Results of the rank test for carbon distribution were clearly influenced by the relatively large species, *Peridinium depressum* Bailey, which was often present but in small numbers. No differences in the diversity (Shannon and Weaver 1949) of the +35 CONC dinoflagellate populations were seen for any depth interval.

The numbers of diatoms counted in the subsamples of the +35 CONC samples studied were generally very small, resulting in wide limits of confidence on the data.

+35 CONC Microzooplankton Taxa

The ciliate protozoan fraction of the 35-μm mesh concentrated samples is dominated by tintinnids. All nearshore tintinnids, with the exception of some individuals of a few species having lorica diameters considerably less than 35 μm, principally of *Tintinnopsis* spp., would be expected to be retained by the netting. Tintinnid abundance was highest within the upper depth interval (surface-15 m) studied, averaging 25.5 $\pm$14.4/liter at the seven stations of the June 1972 cruise and 118.0 $\pm$56.5/liter during the August 1973 study. No dissimilarities between stations to the north or south of the outfall were observed in either tintinnid numerical abundance or carbon for any depth interval of the total water column population except at 15-30 m in June 1972 when stations to the south averaged higher than those to the north. The Mann-Whitney rank test also pointed out this difference for which we have no ecological explanation.

Actinopod sarcodinians, organisms capable of engulfing food particles including small phytoplankton and detritus, were relatively numerous. Radiolarian actinopods averaged 15.4 individuals/liter over the 60-m water column in June 1972 and 25.2/liter in August 1973. The only dissimilar distributions of radiolarians north and south of the outfall were a greater abundance in the 0-15 m samples to the south in June 1972 and to the north in the same depth interval in August 1973. Only the latter was also shown by the rank test. Acantharians, another group of actinopods, showed no differences in abundance at or within sites to the north or south of the outfall on either cruise. Average acantharian abundance (0-60 m) was slightly greater than that of radiolarians in August 1973, being 32.8 individuals/liter, but in June 1972, with an average 9.7 specimens/liter, was lower than that of radiolarians. Greatest acantharian abundance was in the upper depth interval, with a marked decrease in the lower parts of the water column.

The only metazoan microzooplankton group seen in sufficient numbers to give generally reasonable levels of confidence in the data was the naupliar copepods. In June 1972 dissimilar abundance of these developmental stages was found in the 30-45 m depth interval. Stations to the north of the outfall where the ammonia plume and higher seston and ATP levels were evident averaged

18.5 $\pm$5.1 individuals/liter compared to 7.2 $\pm$2.7/liter to the south. This difference was also detectable with the Mann-Whitney rank test. No additional differences were observed between sites north and south of the outfall in either the 1972 or 1973 study.

DISCUSSION

Eppley et al. (1972) considered the timing of their study in June-July 1970 as "propitious" for detecting eutrophication at outfalls. Natural occurrences, such as upwelling, which can also lead to enhanced productivity and greater standing crops, were not important at the time, thus allowing the sewage effluent-induced enhancement to stand out against a background of generally low crops. On both of our cruises, drops in temperature within the upper 10 m of 4-6°C indicated that colder water which might have been expected to be relatively nutrient-rich was reaching into the euphotic zone which Secchi disc readings had suggested was 10-15 m deep. Nutrient determinations, nevertheless (studied in June 1972 only), consistently showed low concentrations of inorganic nitrogen and phosphorous within the euphotic zone, although at stations to the south of the outfall the upper part of the nutricline may have been near the compensation depth. However, if the photosynthetic populations were utilizing the nutrients as fast as they became available, no enhanced levels would be seen. In the study of Eppley et al. (1972), inorganic phosphorus and nitrogen concentrations were uniformly low at both outfall and control stations suggesting nutrient availability was limiting to further production.

The standing crops of phytoplankton, as evidenced by chlorophyll *a* levels, could not be considered very high and thus potentially masking to outfall eutrophication. Even considering the possible loss of chlorophyll in the June 1972 samples at 50% or greater (see Materials and Methods), the values for both cruises were similar to those seen by Eppley et al. (1972) at their control sites off La Jolla and did not begin to approach the high levels they observed at the outfall. Their three sets of data from the control station showed an average chlorophyll *a* level of 0.9 μg/liter over the euphotic zone (average depth, 37 m), whereas at the Point Loma outfall the average level in the euphotic zone (average depth, 21 m) was almost 8 μg/liter. During a 5-month period of approximately weekly observations by the Food Chain Research Group (FCRG) in 1967 at sites 1.4 and 4.6 km offshore of La Jolla, the chlorophyll level through the euphotic zone averaged 1.07 ($\pm$0.86) and 0.65 ($\pm$0.56) μg/liter, respectively (University of California, Institute of Marine Resources 1968). The positions of our outfall stations in terms of water column depth and distance from shore fall intermediate between these two sites.

Direct measurement of primary production was not undertaken during either cruise. The nature of our sampling program with stations being occupied throughout

131

daylight hours would have necessitated productivity incubations starting at various times of the day or else being held for differing lengths of time before starting incubations. Both conditions are undesirable, resulting in problems with interpretation of the data (see discussion in Thomas 1972).

Several other studies of the Point Loma area have also not found higher phytoplankton crops at the outfall. Included is a cruise in June 1971 by the FCRG (Anonymous 1971; Reid 1972). Thomas (1972), who conducted a series of approximately quarterly studies of various southern California outfalls from May 1971-May 1972, saw evidence of eutrophication at Point Loma in only one (June-July 1971) out of four studies. At that time the chlorophyll level through a 15-m euphotic depth at eight sites within a mile of the outfall ranged from 2.7-5.4 μg/liter whereas a site 5 miles (8.1 km) to the north showed 0.8 μg/liter, and other stations off Camp Pendleton (30 miles [48 km] to the north) taken as controls were 0.4-0.8 μg chl a/liter.

An increase in primary crop and secondary stocks sufficient to be detected over background would depend upon the water movement, both lateral transport and vertical displacement, in the area. The general knowledge of circulation in the Southern California Bight has been summarized by Jones (1971). Much of his discussion is of the relatively long-term components (i.e. those measureable on a scale of weeks and months) such as current systems. For surface circulation to 100 m in waters directly adjacent to the coast, a generally southeasterly flow is seen much of the year. Hendricks and Harding (1974) also reported southerly currents both at the surface and in subthermocline waters (39 m) in May 1972, when they followed drogues set out at the Point Loma outfall for two days. Current flow, at least at subthermocline depths, in the opposite direction was indicated in the present study by the ammonia plume which was seen to the NNW of the outfall. Data of Thomas (1972) on ammonia around the Point Loma outfall also indicated northward currents at least at times (e.g. Outfall Cruise 2, June-July 1971).

Superimposed on the long-term flow patterns are shorter term variations. Gaul and Stewart (1960), working in nearshore areas off San Diego, concluded that short-term movements of waters below the thermocline (usually 10-15 m) were primarily tidal, whereas wind was principally responsible for short-term variations in the upper waters. Their study of surface circulation off Point Loma, including the area of the outfall, showed a generally clockwise movement with net *tidal* drift for a 25-hour cycle varying between approximately 1,220 and 3,050 m depending upon the type of tide.

Other parameters of short-term period of possible consequence to our results include internal waves and internal tides of time periods measurable in minutes and hours, respectively. Internal waves, for example, could affect the vertical position of the ammonia plume. Lafond (1963), making observations at a site about 12 km north of the sewage outfall, found over a week in summer that the most common internal waves were of 5.6 feet (1.7 m) with a periodicity of 7.3 minutes. Kamykowski (1974) showed, by computer modelling, the significant effect that the semidiurnal tides along the southern California coast could have on the distributions of various motile and non-motile microplankters. Analysis of the nature of water movements during the present study was beyond the scope of the work. It is clear, however, that as the result of physical phenomena outfall materials or the organisms utilizing them may be dispersed too rapidly to have a discernible effect in terms of crop elevation.

Failure to observe enhanced crops at the outfall would also result if the effluent contained a limiting factor. Thomas (1972) performed some bioassays with outfall surface and sub-thermocline waters using three common local algal species, and, although some inhibition was observed, there was no consistency as to which of the three species tested was inhibited.

Still another possible explanation for the lack of evidence of enhanced productivity and primary crops is that the effluent enrichment did not reach the euphotic zone. The effluent from the outfall diffuser system, although mixing with the surrounding seawater, is at a relatively low density and will rise. At the same time, it may be subject to turbulent mixing and can be dispersed laterally by currents. The dispersed effluent would cease to rise at a depth at which its density and that of the surrounding waters are the same. This depth would be dependent upon the salinity and/or temperature structure of the water column. If at a depth below the euphotic zone (i.e. 15 m) and, hence, the usual level of the strongest part of any thermocline, salinity could be the important determining factor. A salinity minimum at intermediate depths is characteristic of the area and was seen at the stations studied in June 1972 at depths of 20-40 m. Salinity at its minimum was 33.51 ppt (average, Stations 1-7), whereas at the surface and bottom (i.e. 60 m) average salinities were 33.68 and 33.66 ppt, respectively. It is possible that vertically migrating phytoplankton could utilize the effluent ammonia at intermediate depths (see discussion in Hendricks and Harding 1974), but their subsequent dispersion may be too rapid to be seen as enhanced standing crops. It can also be noted that depending upon the physical characteristics of the effluent and surrounding waters, the effluent materials might be maintained in a thin layer, and their detection by the relatively widely spaced water bottle sampling used here, as well as by Eppley et al. (1972)

and Thomas (1972), is subject to a degree of chance.

During the June 1972 cruise, at least, the outfall plume of enriched water was detectable as a recognizable entity, principally by its content of ammonia. Although only inorganic materials were measured, it can be suggested that dissolved organic materials may also have been higher in the plume. In addition to the evidence we saw of higher-than-average abundance of total seston and elevated ATP in the depth interval that included the plume, Carlucci (personal communication) found enhanced vitamin levels, principally B_{12}, in the same waters. Dissolved vitamins are known to be the products of both phytoplankton (e.g. Carlucci and Bowes 1970) and bacteria (e.g. Haines and Guillard 1974). Further, Carlucci and Shimp (1977) reported an approximate order-of-magnitude greater growth of low-nutrient bacteria at the 40-m depth of Station 1, where high ammonia levels were found, relative to 20- and 60-m samples. Thus, even though discernible effects of outfall eutrophication may not be apparent in the photosynthetic populations of the euphotic zone, there may be increased biological activity centered on the nutrient plume. Its magnitude, the number of trophic levels represented, and the discernible extent would depend upon the length of time the integrity of the effluent is maintained.

Although a number of studies have been undertaken in recent years to look for signs of eutrophication at the Point Loma outfall, the total is still relatively small. However, the results are sufficient to suggest that discernible evidence of outfall eutrophication may be unusual and of a very transitory nature. To obtain a more accurate evaluation of the importance of outfall eutrophication effects on biological production in San Diego coastal waters would, as strongly suggested by Hendricks (1975), require a monitoring program with a much more frequent and regular periodicity than the extremely sporadic and short-term observations characterizing the efforts to date.

ACKNOWLEDGMENTS

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CONVERSION ALGORITHMS FOR THE CALCOFI STATION GRID

L.E. EBER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, CA 92038

ROGER P. HEWITT
National Oceanic and Atmospheric Administration Corps
Southwest Fisheries Center
La Jolla, CA 92038

ABSTRACT

This note presents algorithms which may be used to convert station positions expressed in geographic coordinates (latitude and longitude) to the California Cooperative Oceanic Fisheries Investigations (CalCOFI) station grid coordinates and vice versa. Clarke's spheroid of 1866 is used as an estimate of the geoid off the west coast of North America.

INTRODUCTION

The CalCOFI station pattern (Figure 1) was designed orginally in the development of a systematic sampling program to determine the major spawning areas of the Pacific sardine off the coasts of the United States and Baja California, Mexico. Surveys were conducted along lines extending seaward approximately normal to the coast and spaced 120 miles apart from the Columbia River to Sebastian Vizcaino Bay. As the program progressed and spawning areas were delimited, additional lines of stations were added between the cardinal lines, and the surveys became concentrated off the coasts of California and Baja California.

The pattern was based on line 80 off Point Conception, California. Other lines were numbered using increments of 10, decreasing northwestward to line 10 off the U.S.-Canadian border, and increasing southeastward to line 157 off Cape San Lucas, Baja California (Kramer et al. 1972). It was originally intended that the 120-mile spacing would allow for additional lines to be plotted 12 miles apart between the cardinal lines and still be designated by whole numbers without resorting to fractions. However, when it was decided to insert additional lines, 40-mile intervals appeared to be sufficient. Thus the major pattern consists of cardinal lines in numbered multiples of 10 and ordinal lines whose numbers by convention end in 3's and 7's, having been rounded off from 3.333. . . . and 6.666. . . . .

The stations on the lines were laid out on the basis of a perpendicular to line 80, through a point designated Station 80.60. The original stations were plotted 40 miles apart and were numbered by increments of 10, which allowed additional stations between the 40-mile points to be plotted as close to 4 miles and still be designated by whole numbers.

CONVERSION OF CALCOFI GRID COORDINATES TO GEOGRAPHICAL COORDINATES

The primary reference point, Station 80.60, was located at 34°09'N, 121°09'W and is marked 0 in Figure 1. The perpendicular to line 80, through this point, was used to set all the other lines and will be referred to in the following discussion as the reference line.

As indicated before, unit line number increments represent 12 nautical miles and unit station number increments represent 4 nautical miles. Therefore, to locate a particular station, such as 50.120 (designated P in Figure 1), one would first proceed 360 nautical miles northwestward along the reference line from the reference point to Station 60 on line 50 (designated R in Figure 1), and then 240 nautical miles southwestward on line 50 to Station 120.

The CalCOFI station plan was originally laid out in this manner with the aid of navigation and plotting charts. CalCOFI station locations can also be computed numerically, using the Mercator transform based on Clarke's spheroid of 1866, as given by Bowditch (1958). The numerical procedure can be derived from the geometry of Figure 1, bearing in mind that distance along the Y-axis (north-south) on a Mercator chart must be measured in meridional units rather than in units of latitude.

Let PLA   =   Latitude of P
    PLO   =   Longitude of P
    PLN   =   Line number of P
    PSN   =   Station number of P
    RLA   =   Latitude of R
    MCTR(LA)   =   Mercator transform

which expresses the distance from the equator to latitude LA and is defined by:

$$MCTR(LA) = (180/\Pi)*(LN(TAN(45 + LA/2)) - 0.00678766*SIN(LA))$$

This is an approximation, accurate to within 3 seconds (in meridional units) south of 60°N. Recalling that the CalCOFI coordinates of the primary reference point are 80 (line number) and 60 (station number) and the geographical location of this point is 34°09'N, 121°09'W, the following sequence can be used to compute the location of P.
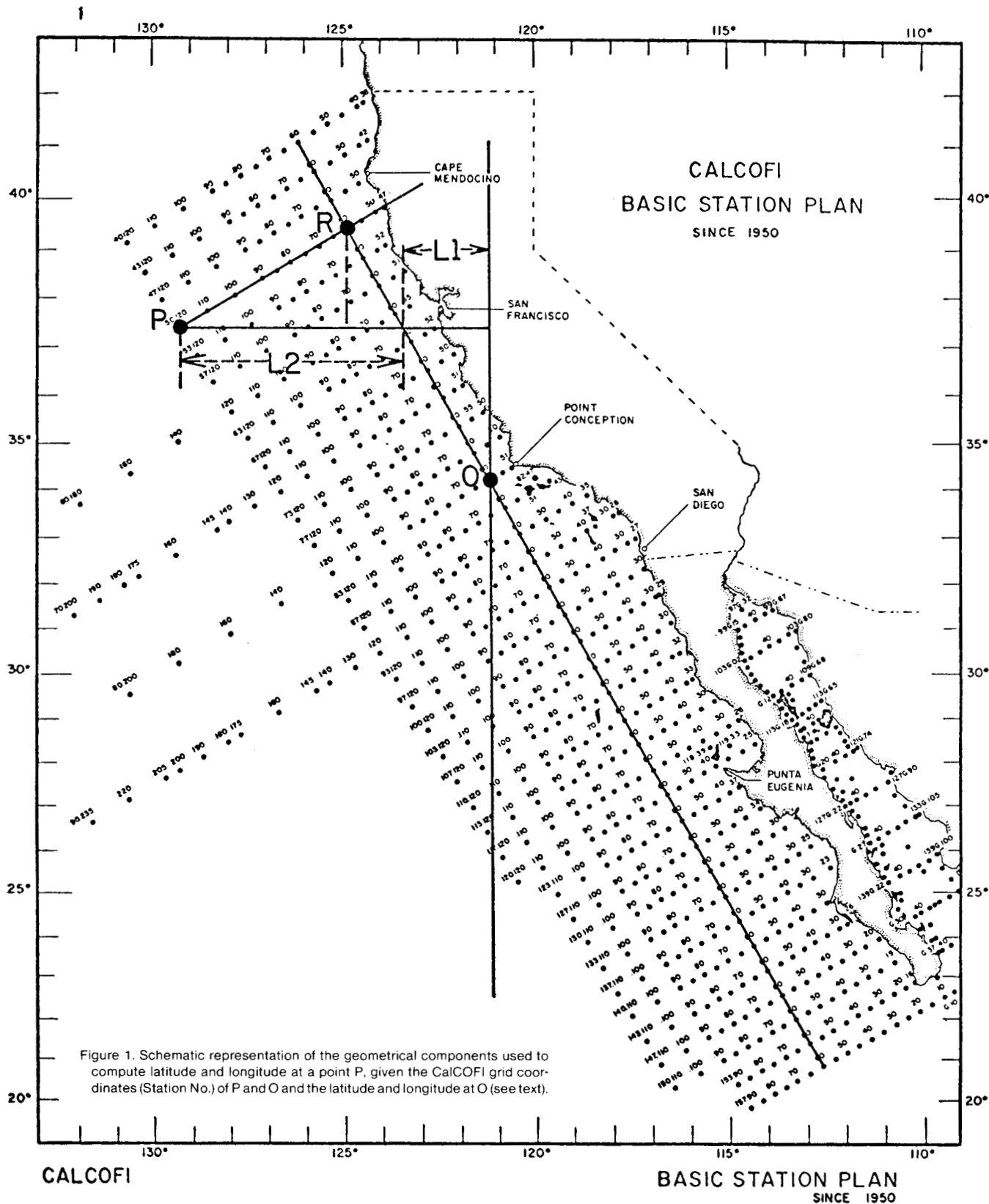
Figure 1. Schematic representation of the geometrical components used to compute latitude and longitude at a point P, given the CalCOFI grid coordinates (Station No.) of P and O and the latitude and longitude at O (see text).

1. RLA = 34.25 − 0.2*(PLN − 80)*COS(30)
2. PLA = RLA − (1/15)*(PSN −60)*SIN(30)
3. L1 = (MCTR(RLA)−MCTR(34.15))*TAN(30)
4. L2 = (MCTR(RLA)−MCTR(PLA))/
   (COS(30)SIN(30))
5. PLO = L1 + L2 + 121.15

CONVERSION OF GEOGRAPHICAL COORDINATES TO CALCOFI COORDINATES

The computation of CalCOFI line and station numbers for a given location where latitude and longitude are given requires determination of a latitude when its Mercator transform is known, i.e. given MCTR(LA), find (LA). There is no simple algebraic solution to this problem; however, (LA) can be approximated with as much precision as desired with a simple iterative procedure in which MCTR(LA) is entered as the first approximation to (LA). The algorithm for the inverse Mercator transform is as follows:

1. Set I = 0
2. Set LA = MCTR(LA)
3. LA = 2*(ARCTAN(EXP(MCTR(LA)*II/180 +
   0.00676866*SIN(LA)))−45)
4. I = I + 1
5. IF I < 3 GO BACK TO STEP 3
6. STOP

The CalCOFI grid coordinates for a station at a given location can be computed with the following sequence:

1. L1 = (MCTR(PLA)−MCTR(34.15))*TAN(30)
2. L2 = PLO − L1 − 121.5
3. MCTR(RLA) = L2*COS(30)SIN(30) +
   MCTR(PLA)
4. RLA = INVERSE(MCTR(RLA))
5. PLN = 80 − (RLA − 34.15)*5/COS(30)
6. PSN = 60+ (RLA−PLA)*15/SIN(30)

DISCUSSION

The two conversion procedures presented here are mutually consistent in that when executed consecutively, using the output from one run as input for the next, the original coordinate values can be recovered with a precision of at least four decimal places. For example, Station 50.120 converts to 37° 20.7692′N, 129° 16.7727′W. With these values as input, the reciprocal conversion yields 50.0000 and 120.0000 for line and station, respectively. However, if the geographical coordinates are rounded to tenths of minutes, as is common in CalCOFI work, the conversion to line and station becomes 49.9969 and 120.0004.

We should point out that the correspondence between CalCOFI and geographical coordinates as computed from the numerical procedures is not in exact agreement with that given in the standard reference tables used by CalCOFI. The discrepancies are generally less than 2 minutes of latitude or longitude for given CalCOFI station numbers except out on the fringes of the pattern. They may possibly be due to accumulative errors incurred when laying out the station pattern on the navigational charts.

It should further be noted that even greater discrepancies are found when the computed locations for CalCOFI stations are compared with the actual locations occupied on individual cruises, as reported in the CalCOFI Physical and Chemical Data Reports. Deviation from standard station positions may have occurred during CalCOFI cruises to avoid navigational hazards or other reasons and nearby alternate locations accepted as representing the designated station. The conversion procedures can provide a convenient way to determine the CalCOFI coordinates of the actual locations occupied in such instances.

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USE OF AIRBORNE RADIOMETERS FOR MONITORING SEA SURFACE TEMPERATURE AND CHLOROPHYLL IN A COASTAL FISHING ZONE

MERRITT STEVENSON
Inter-American Tropical Tuna Commission
Scripps Institution of Oceanography
University of California San Diego
La Jolla, CA 92093

JAMES SQUIRE, JR.
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, CA 92038

CHARLES BOOTH
Institute of Marine Resources
Scripps Institution of Oceanography
University of California San Diego
La Jolla, CA 92093

YOSHIMINE IKEDA
Universidade de São Paulo
Caixa Postal, 9075
São Paulo, Brasil

ABSTRACT

The need for monitoring the rapidly changing coastal marine environment and using this information in the assessment of a coastal fishery such as the California anchovy is noted. Previous measurements of sea surface temperature and relative chlorophyll concentration suggest that these are two important biological parameters that can be rapidly obtained in a synoptic fashion from a suitably equipped aircraft. Experimental flights with a twin engine Beechcraft Travel Air aircraft equipped with a modified precision radiation thermometer (PRT-5) infrared radiometer and a dual channel differential radiometer (DCDR) for ocean color were made on several occasions in late 1974, and the results from the 4 and 9 October flights are briefly described. Analysis of these flight data suggest that by careful evaluation of the strip chart records, statistically significant relationships can be obtained between both remote sensors. While quantitative results depend upon reasonably frequent ground-truth observations for both radiometers, particularly the DCDR instrument, a rough conversion to mg chlorophyll/m^3 for the DCDR was made based on limited surface chlorophyll a measurements and published calibration curves. The results suggest that when the design constraints of the DCDR instrument are recognized and the instrument is used in conjunction with the PRT-5 radiometer the paired radiometers offer considerable potential for monitoring two biologically important parameters in a coastal fishing zone.

RESUMEN

Se indica que es necesario supervisar los cambios rápidos que se presentan en el ambiente marino costero y usar esta información en la pesca superficial, como es la pesca de la anchoveta californiana. Las medidas tomadas anteriormente de la temperatura superficial del may y, de la concentración relativa de clorofila indican que estos son dos parámetros biológicos importantes que pueden obtenerse rápidamente de una manera sinóptica desde un avión equipado convenientemente. A fines de 1974 se realizaron en varias ocaciones vuelos experimentales con un bimotor Beechcraft Travel Air, equipado con un radiómetro modificado infrarojo PRT-5 y un radiómetro diferencial de doble banda (Dual Channel Differential Radiometer [DCDR]) para obtener datos sobre el color del océano, y se describen brevemente los resultados de los vuelos realizados entre el 4 y 9 de Octubre. El análisis de los datos de estos vuelos indican que al evaluar cuidadosamente los registros del aparato de banda, se pueden obtener relaciones estadísticamente significativas entre los dos sensores remotos. Aunque los resultados cuantitativos dependen de las observaciones terrestres reales, obtenidas con frecuencia razonable de ambos radiómetros, especialmente del instrumento (DCDR), con respecto a este instrumento se hizo una conversión preliminar a mg de la clorofila/m^3 basadas en medidas limitadas de la clorofila a en la superficie y de publicaciones de las curvas de calibración. Los resultados indican que cuando se reconocen las limitaciones del trazado del instrumento DCDR y se usa éste junto con el radiómetro PRT-5, los dos radiómetros ofrecen un potencial considerable para la supervisión de los dos parámetros biológicamente importantes en una zona costera de pesca.

INTRODUCTION

Both coastal fisheries and pelagic fisheries respond to changes in the environment, but coastal conditions may frequently undergo greater changes than conditions in the open ocean. The famous anchovy (*Engraulis ringens*) fishery off Peru is located in a coastal upwelling regime where horizontal surface temperature gradients of 3°C/ 50 km may occur and give rise to fluctuations in the phytoplankton populations and corresponding surface chorophyll gradients of 3 mg/m^3 (Beers et al. 1971). Higher trophic levels such as the anchovy are in turn dependent upon the standing crop of the phytoplankton. An adequate understanding of the presence and variability of a regional coastal fishery, then, depends upon the scientists' ability to monitor the rapidly changing environment and to determine how coastal fish stocks respond to these changes in the environment.

Two of the more important parameters used to monitor the marine environment are surface temperature (may indicate relative intensity and duration of upwelling) and chlorophyll (estimates standing crop of phytoplankton). In principle it would be desirable to make weekly, if not daily, ship surveys of the coastal zone to monitor these and other important parameters. In most instances, however, ship time is expensive and, therefore, limits such surveys to several-day cruises. A method that can rapidly scan a long coastal zone and provide environmental data of reasonable accuracy would represent an optimum method of obtaining the needed environmental information in order to make indirect assessment of some fish stocks of the coastal waters. Stevenson and Miller (1974) have correlated tuna fish catch with sea surface temperature in a region 1800 km west of California, although cloud cover was a problem. Intervening clouds may be more of a problem in coastal zones, and in those regions a low-flying aircraft using remote sensors may be ideally suited for the job.

Airborne survey flights to assess apparent fish abundance have been made commercially for a number of years. Squire reports (1972) that it is feasible to estimate fish school tonnage from commercial spotter aircraft flights over the coastal zone of California from the Los Angeles Bight south to the Mexican border. Squire's study is based on more than 17,000 flight hours made during 1962-69. More recently Squire has made survey flights to monitor sea surface temperature patterns for correlation with change in catch and catch rates for several coastal species. Sea surface temperatures were determined with a Barnes' PRT-5 radiometer from an aircraft. Arvesen et al. (1973) have developed an extremely compact instrument for detecting changes in ocean color, the dual channel differential radiometer (DCDR). He has flown the DCDR and PRT-5 radiometer off the California coast where, during an offshore transect, he obtained an inverse pattern between sea surface temperature and chlorophyll concentration.

During September-October 1974, a visit was made by Professor Ikeda to the Inter-American Tropical Tuna Commission (IATTC) headquarters, at the National Marine Fisheries Service (NMFS) Laboratory in La Jolla, to investigate methods of using airborne and spacecraft data in the field of fishery oceanography. After some discussions by the first two authors with Ikeda, several instructional/experimental flights using the NMFS PRT-5 radiometer were made off the southern coast of California. It then came to our attention that Dr. Arvesen's DCDR ocean color radiometer was on loan to Mr. Booth of the Institute of Marine Resources (IMR), and we invited Mr. Booth to participate in joint flights where both the DCDR and PRT-5 instruments might be flown together.
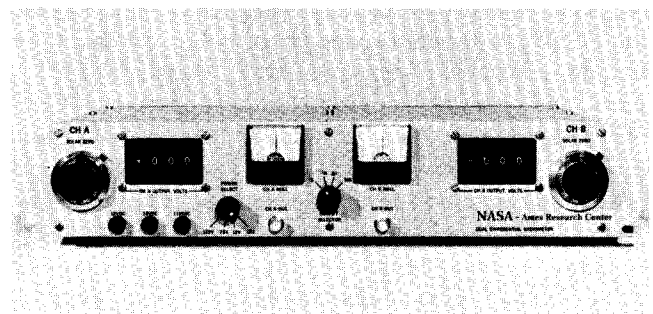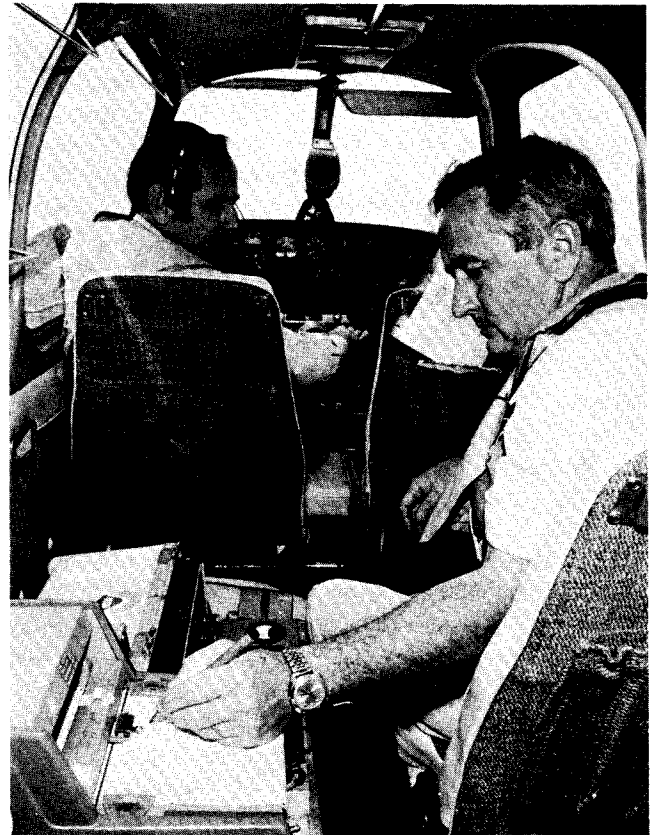
Figure 1. (Upper) Modified precision radiation thermometer (PRT-5) mounted in aircraft. Scientific observer sits in opposite seat to make time and position annotations on charts produced by the PRT-5, and the (lower) dual channel differential radiometer (DCDR).

INSTRUMENTS AND METHODS

Two radiometers were used from the aircraft normally chartered by NMFS for its sea surface temperature survey flights, etc. (Figure 1). The NMFS instrument, a modified PRT-5 radiometer equipped with a 10.5-12.5 micron filter, together with a strip chart recorder and power supply, were mounted to a miniature instrument rack. The rack was attached to the positioning frame of a passenger seat in the rear of the plane after the seat had been removed from the aircraft. The access port for instruments was located directly behind the rear cabin bulkhead and was reached by

removal of the bulkhead prior to the flights.

The DCDR instrument was developed by Dr. John Arvesen of the NASA/AMES Center and was available through his courtesy for field experiments. Because a detailed description of the system's specifications is found in Arvesen et al (1973), only a brief explanation is given here. The DCDR is a rack-mounted, all solid-state instrument and requires a conventional strip chart recorder for output. The color sensor consists of a wide-angle field of view lens cemented to one end of a fiber optics cable. The fiber optics bundle is split at the other end into four smaller bundles. Each of these is arranged so that the emerging light passes through a narrow band interference filter and strikes a silicon diode detector. The chlorophyll sensing is accomplished by use of two of these detector-filter combinations. One combination uses a 525-μm band-pass filter for the reference signal as this is the wavelength region of minimum attenuation due to chlorophyll. The other detector-filter combination has a 443-μm band-pass filter which is an absorption maximum for chlorophyll a. The ratio of the light from the fiber optic bundle striking these detector-filter combinations is calculated by the instrument and displayed on a strip chart recorder. During an experiment the probe is pointed downward at an angle (approximately 15°) to minimize the reflected glitter on the ocean surface. The probe is occasionally pointed at or toward an unobstructed view of the sun during each flight, and the DCDR instrument's gain is normalized at that time. For the experiments described in this paper, the PRT-5 instrument rack was modified to accommodate the DCDR instrument and a Hewlett Packard Mosley strip chart recorder. The power for both PRT-5 and DCDR instruments was obtained from the aircraft's electrical generators. For simultaneous operation of the two radiometers, a cylindrical flange was made and attached to the circumference of the access port so that the narrow beam PRT-5 sensor head was axially aligned through the port. Special slots were cut into the flange to accommodate the DCDR probe. While the two probes were not exactly coaxially aligned, the wide-angle field of view of the DCDR probe assured adequate overlap of the viewing targets of the two radiometers.

The principal problem with the DCDR is its dependence on constant solar illumination of the sea surface. This problem has two parts. First, atmospheric conditions must be uniform over the flight path so that the spectral composition and intensity of the light incident on the sea surface remains constant. This drawback may be compensated for by repetitive standardization by viewing the sun with the probe. This limits flights to days with uniform clearness. The second problem arises when the airplane changes headings, thus changing the probe viewing angle relative to the angle of the sun and resulting change in the amount of back reflection or "glit-

ter" from the sea surface. Efforts to compensate for this effect by changing the position of the probe are never wholly satisfactory. This effect tends to bias the signal to the null position, which corresponds to 1 mg/m³ chlorophyll a. It is very difficult to correct for this effect on the present instrument, although we hope to make certain modifications in the future to reduce the instrument's sensitivity to glitter.

Calibration for the PRT-5 was provided by flying over the Naval Electronics Laboratory (NEL) tower located about 3 km offshore from San Diego. In previous flights with the NMFS PRT-5 instrument, Squire found the corrected airborne temperature data to be within 0.1-0.2°C of temperatures measured from the NEL tower. The calibration of the DCDR instrument was accomplished in a similar fashion. The DCDR does not provide readout directly in units of chlorophyll but rather in volts. To convert the volts into mg chlorophyl a/m³, one or more surface water samples are collected beneath the flight path and chemically analyzed for chlorophyll a concentration, and the DCDR data are then converted from volts into chlorophyll units.

FIELD EXPERIMENTS

Because the time available to make the cooperative flights fell within the time frame of the NMFS sea-surface temperature survey flights, we decided to use the NMFS flight track to make simultaneous measurements with both radiometers. One observer sat in the starboard rear seat in order to operate the radiometer recorders mounted on the port side; a second observer sat in the co-pilot's seat and assisted with general flight operations. Flights using both PRT-5 and DCDR instruments were made on 4 and 9 October 1974. The same general flight plan was followed each time. Since the flight observations were also similar, only the October 4 flight will be discussed. The aircraft flew from a local San Diego airport over the coastal water at 150 m altitude starting at 1150 PDT, and the flight track was terminated at 1330 PDT after which the aircraft returned to the same airfield. During the flight the aircraft flew over the NEL tower twice to obtain sea surface calibration temperatures for the PRT-5 data. The DCDR uses a solar reference, and during cloud-free conditions, when properly normalized, provides a reasonably stable output signal. During the flight a calibration of the DCDR was conducted by twice passing over a boat where surface water sample was collected for chlorophyll a analysis. The boat was located about 1.5 km off the Scripps pier.

RESULTS

After the 3.5-hour flight, the strip chart records were checked for proper time and position annotations, and the charts were then manually digitized. PRT-5 data
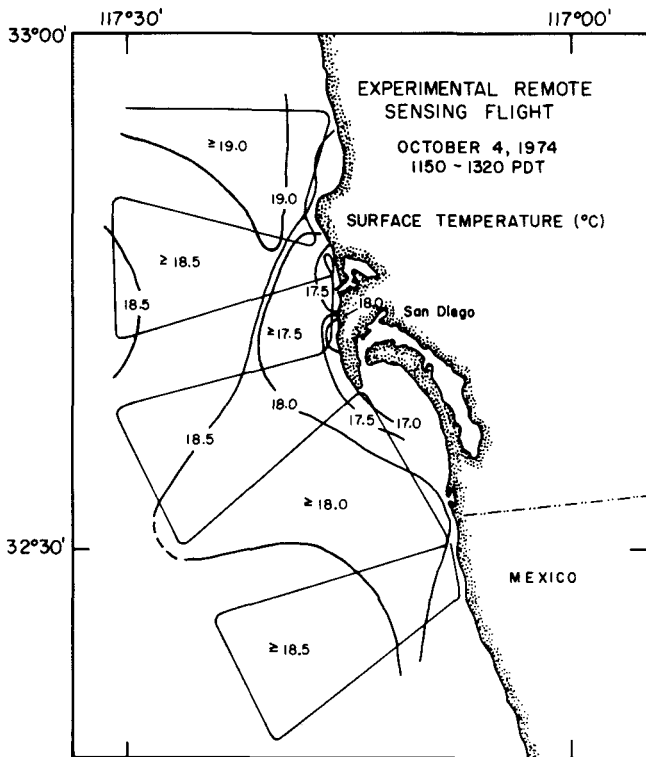
Figure 2. Sea surface temperature map for 4 October 1974, based on Barnes PRT-5 radiometer data. Blackbody thermal radiation is measured continuously as the aircraft moves along its flight path.
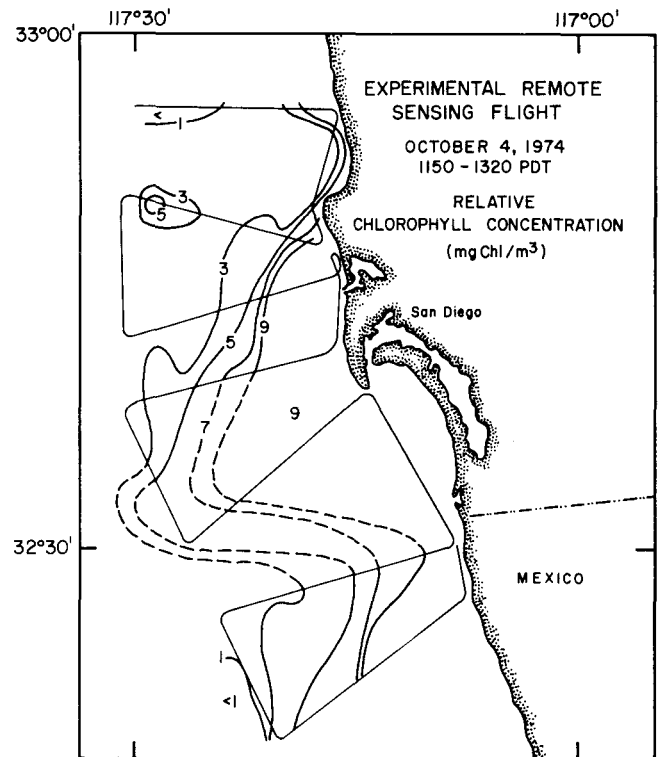

Figure 3. Relative chlorophyll concentration map for 4 October 1974, based on the DCDR ocean color instrument data. The intensity measurements of 443 μm ocean color, which change in response to chlorophyll concentration are referenced to 525 μm radiation, which undergoes minimal change due to the presence of chlorophyll.

were calibrated with the NEL tower temperature data, and the calibrated temperatures were used to construct a contoured map of the surface temperature shown in Figure 2. Ocean color data from the DCDR instrument was similarly digitized and calibrated with the surface chlorophyll measurements off Scripps Pier, and the data were used to construct the surface chlorophyll map shown in Figure 3.

For statistical purposes, the analog records were read at 1-minute intervals to form data pairs. A comparison of the PRT-5-derived surface temperatures and DCDR-derived Chlorophyll Index data (CI) obtains a correlation coefficient for the 4 and 9 October experiment of $r = -0.49$ and -0.60 ($P = 1\%$ level), respectively, and the following relationships:

$$CI = -0.58T + 21 \text{ and}$$
$$CI = -0.55T + 12.8$$

respectively, where the slopes are the conversion constants from Chlorophyll Index (volts) to surface water temperature. Analysis of the individual strip charts shows considerable "small structure," appreciable gradients in temperature that extend over distances of several hundreds of meters. Because one surface measurement of chlorophyll was made on 4 October, it was only possible to roughly calibrate the DCDR data. The result of the

calibration is based on data from Arvesen et al. (1973) and for $0 < CI < 3$ volts is

$$chl\ a = 0.58(CI - 7.6)^2 + 1.2,$$

where 0.58 is the conversion rate from volts to 1.2-6.5 mg chl a/m^3 and 7.6 and 1.2 are voltage and recorder curve offsets. For lower concentration levels, i.e. $0.1 < chl\ a < 1$ mg/m^3, an approximate conversion is

$$chl\ a = 0.027\ (CI - 1.4)^2 + 0.092.$$

It should be recognized that the conversion from Chlorophyll Index to chl a is only approximate unless the conversion can include the effects of non-chlorophyll suspended sediment and more calibration points.

Due to a lack of fish school sightings during the flights, it was not possible to compare locations of fish schools with thermal and chlorophyll fronts. Squire, however, has noted (manuscript 1975) that when albacore concentrations are present and observed off central California, they are often found on the seaward (warm) side of thermal fronts. Other studies, e.g. Stevenson and Miller (1974), have shown that tropical and subtropical tunas are frequently found along edges of pronounced

141

thermal gradients or fronts. Because anchovy, at least in their early life, feed first upon phytoplankton and later upon zooplankton which in turn feed upon phytoplankton, it is important to make comparisons of apparent abundance of anchovy schools relative to concentrations of chlorophyll (phytoplankton). Aircraft surveys similar to those described in this paper may determine whether or not distribution of anchovy larvae and adult schools off southern California and Baja California is related to measurements made with infrared radiometry and airborne ocean color radiometer without the measurements of the intermediate zooplankton trophic level. Thus far no researchers have shown the feasibility of directly monitoring zooplankton by remote sensor. The question to be answered is whether or not information on zooplankton abundance must also be available or whether sufficient information about the presence of the anchovy can be obtained from aerial infrared and multispectral radiometry. Future airborne survey flights are needed to address this question.

ACKNOWLEDGMENTS

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ASSESSMENT OF A LARGE-CAPACITY FISH PUMP FOR SAMPLING ICHTHYOPLANKTON FOR POWER-PLANT ENTRAINMENT STUDIES

J.A. ELDER[1]
Tetra Tech, Inc.
Lafayette, CA 94549

J.W. ICANBERRY
Director of Engineering Research
Pacific Gas & Electric Company
3400 Crow Canyon Rd.
San Ramon, CA 94583

D.J. SMITH[2]
Tetra Tech, Inc.
Lafayette, CA 94549

D.G. HENRIET
Tetra Tech, Inc.
Lafayette, CA 94549

C.E. STEITZ
Department of Engineering Research
Pacific Gas & Electric Company
3400 Crow Canyon Rd.
San Ramon, CA 94583

Plankton nets are the traditional method for sampling planktonic organisms that are sparsely represented in the water column. However, there are situations where nets are impractical. Such is the case for sampling from the intakes and outfalls of electric generating plant cooling water systems (CWS). Recent federal regulations have required power companies to assess the performance of their once-through cooling systems in terms of biological damage. In order to determine the densities and species of ichthyoplankton entrained in the CWS of two power plants in California, we have utilized a commercial bladeless fish pump.

The applicability of pumps for sampling plankton was discussed as early as 1948 (Welch 1948). However, up to the present time there have been relatively few applications of pumps to plankton sampling. Plankton pumps have been designed, used, reported in the literature, and commercially built (Aron 1958, 1962; Beers et al. 1967; Lenz 1972; Icanberry and Richardson 1973), but they all have had a capacity of less than 1.0 m³, which effectively precludes their use for capturing ichthyoplankton, which is usually present in concentrations of less than one individual/m³. Therefore, we have utilized a pump that has a large enough capacity to obtain samples containing adequate numbers of larval fish for statistical analyses. This pump exhibits minimal avoidance by larval fish and *Neomysis* sp. It delivers 3.0 m³ min⁻¹ at a 3-m head, and in excess of 4.3 m³ min⁻¹ at lower heads.

The pump is a PACO centrifugal, single-port bucket-type design and is marketed by Neilsen Metal Industries, Salem, Oregon. As adapted by Neilsen, the pump is sold as a fish pump for hatchery and aquaculture uses. According to the manufacturer, the pump can lift 30-cm trout 3 m (distance from water surface to pump) with 99.5% survival. It is powered by a one-cylinder, 12-horsepower Wisconsin engine which is powerful enough to deliver the full capacity of the pump. However, a 24-horsepower Onan twin-cylinder engine, which is also available, would delivery the same capacity with less

effort.

From the factory, the pump comes mounted on a small trailer. We designed and installed a collection box on the trailer (Figure 1; numbers in text refer to portions of pump as illustrated). The inside volume of the box is approximately 2 m³. A 505-μm mesh net is suspended in the box during sampling operations (Number 10). The net is framed with anodized aluminum, thus preventing the net from being sucked into the discharge ports (Number 3). A bucket collector at the cod end of the net is used to concentrate the sample.

In order to measure the flow rate, we designed a square weir (Number 4) for the collection box. Field calibration tests show that the observed heights on the weir are very close to actual flow rates (Figure 2). A hook-type gage might provide greater precision in flow rate measurements.

Theoretically, with the use of an auxiliary electric vacuum pump (Number 8) the pump can be primed to a 9.0-m head. It is unknown whether the pump can operate at this head; however, we have pumped a 3.5-m vertical lift at this capacity of 3.0 m³ min⁻¹.

The intake pipe is 15.2-cm diameter aluminum pipe and 4.57 m long. Additional sections 1.5 m long are provided for obtaining greater length if needed.

The discharge pipe (Number 3) from the pump to the collection box is 25.4-cm diameter aluminum pipe. This was designed to reduce the velocity of the water as it enters the net.

Two 20.3-cm diameter discharge pipes drain the collection box. The outlets are located in a smaller box which collects the water flowing over the weir. They insure that the water does not back up and interfere with water-level readings on the weir.

We are presently using the pump to sample larval fish and small crustaceans (i.e. *Neomysis mercedis*). They are collected from the CWS intakes at the circulating water pump suction pits of two different power plants.

Additional studies were conducted to compare the sampling efficiency of the pump to that of a towed 1.0-m 505-μm mesh nylon net. The net was towed across the mouth of the intakes several feet from where the pump
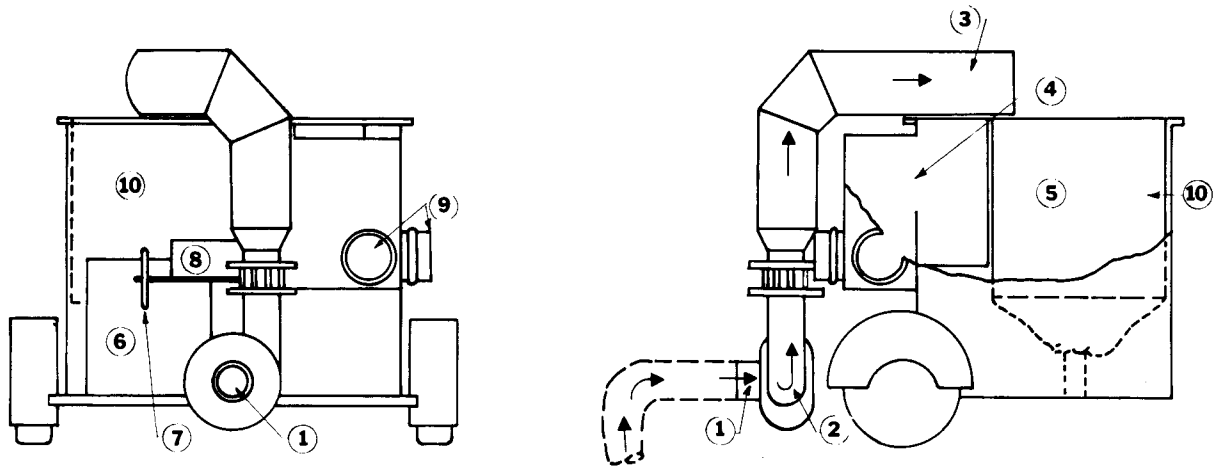
Figure 1. Schematic of pump. 1) intake port, 2) pump body, 3) discharge pipe, 4) weir, 5) tank, 6) engine, 7) gate valve, 8) auxiliary electric vacuum pump for priming, 9) discharge ports, 10) net.

was operating. The results indicate that the pump and net capture statistically similar densities of fish larvae, but the pump was significantly more efficient than the net in capturing *N. mercedis* during 20 paired net and pump samples.

Since the purpose of our ongoing larval fish and *N. mercedis* study is to determine their densities entrained by the power plant cooling systems, we did not address the ability of the pump to capture live organisms. However, the condition of the pumped specimens is such that both larval fish and *N. mercedis* are highly identifiable and in the same physical condition as netcaptured specimens.

The pump can be removed from the trailer and mounted on a boat for open-water sampling. Sampling collection is accomplished by discharging the water over the side of the boat into a net suspended in the water.

The fish pump is an excellent sampling tool in situations where mobility required for conducting net tows is absent. It has proven to be a very reliable, easy-to-operate sampling tool. Its sampling efficiency is equivalent or better than that of net tows in the vicinity of power
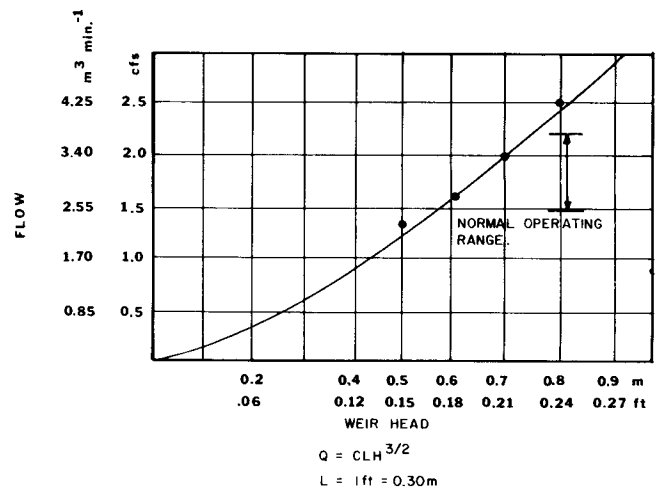
Figure 2. Rated flow curve for weir, Points indicate actual measured flow rate.

plant intakes. We feel that the pump is an entirely satisfactory tool for assessing the density of organisms entrained in power plant cooling water systems.

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DISTRIBUCION VERTICAL DE TEMPERATURA, SALINIDAD, Y OXIGENO DISUELTO EN LA BAHIA DE LA PAZ, BAJA CALIFORNIA SUR, DURANTE LA PRIMAVERA DE 1976

AMADO VILLASEÑOR-CASALES
Centro de Investigaciones Biológicas, A.C.
La Paz, Baja California Sur
Mexico

ABSTRACT

Graphs of vertical distribution of temperature, salinity, and dissolved oxygen in Bahía de La Paz, Baja California Sur, are presented. The data were collected during a cruise aboard the schooner *Queen Mab* in the spring of 1976.

The mixed layer extended to a depth of about 20 m. There was evidence of a thermocline, but the halocline was not well represented. The data showed no upwelling in the bay. High dissolved oxygen values found in surface layers were produced by agitation of the seawater surface by strong winds observed during the cruise. The oxycline was not well represented.

RESUMEN

Se presentan en este trabajo gráficas de distribución vertical de temperatura, salinidad y oxígeno disuelto en la Bahía de La Paz, Baja California Sur. El crucero fue realizado a bordo de la goleta *Queen Mab* durante la primavera de 1976, por el Departamento de Biología Marina del Centro de Investigaciones Biológicas de Baja California, A.C.

La capa de mezcla presentó una profundidad promedio de 20 m. Hubo evidencias de termoclina, mientras que la haloclina no estuvo bien representada. No se presentaron surgencias en ninguna parte de la Bahía. Los altos valores de oxígeno disuelto en las capas superficiales fueron el resultado del intenso oleaje producio por los fuertes vientos observados durante el crucero. No estuvo bien representada la oxiclina.

INTRODUCCION

El Departamento de Biologia Marina dependiente del Centro de Investigaciones Biológicas de Baja California, A.C., efectuó un crucero hidrográfico los días 25 y 26 de abril de 1976 en la Bahía de La Paz (Figura 1). Dicho crucero se realizó a bordo de la goleta *Queen Mab*, la cual fué cedida por la Asociación Científica Océana, A.C. Desafortunadamente no pudo completarse el crucero como estaba planeado debido a fallas tanto en el motor principal como en el motor auxiliar de la goleta y por lo tanto no se efectuaron los hidrolances de las estaciones 25, 26, 27, y 28. En las restantes, los lances de botellas Nansen se hicieron a profundidades estandard hasta los 50-m o bien conforme la profundidad lo permitió.
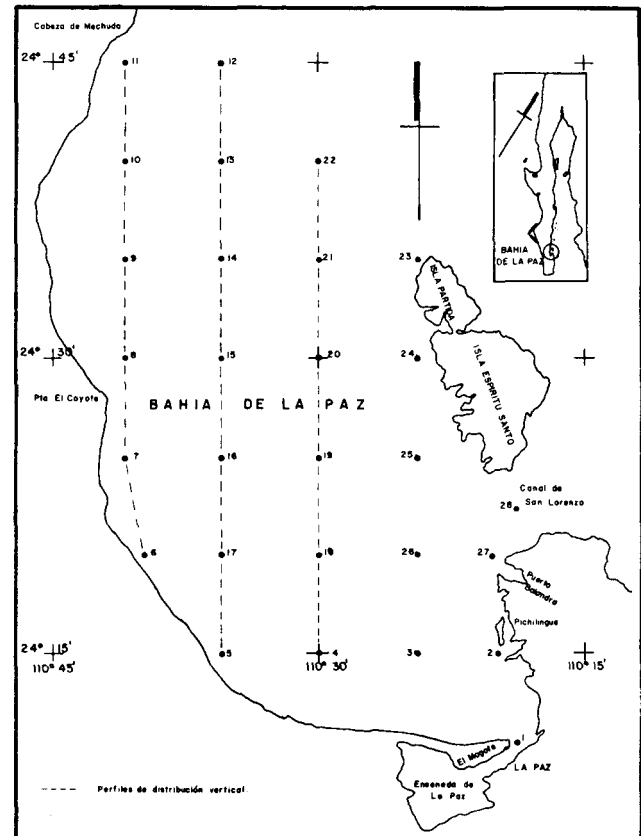
Figura 1. Localización del area de estudio y plan de estaciones del crucero QM-7601.

Como el Departamento de Biologia Marina también está realizando estudios hidrobiológicos estacionales en la Ensenada de La Paz, los datos obtenidos en la Bahía se pueden utilizar como comparación y referencia con los estudios que se obtengan dentro de la Ensenada. También pueden correlacionarse con futuros estudios que se hagan dentro de la misma Bahía.

METODOS

Para la obtención de los datos de temperatura (°C) se siguió el método del Marine Technician's Handbook (Anonimo 1972). Los datos de salinidad (°/oo) se obtuvieron por medio de la determinación de clorinidad utilizando el método de Knudsen (Oxner 1920) y su posterior conversión a salinidad, empleando las tablas hidrográficas de Knudsen. Los valores de oxígeno disuelto

(ml/litro) se determinaron por medio del método macro-Winkler descrito por Strickland y Parsons (1972).

DISTRIBUCION VERTICAL DE PROPIEDADES
Temperatura

En las gráficas de distribución de temperatura (Figura 2), los rasgos más sobresalientes son la termoclina y la profundidad de la capa de mezcla. Para el primer transecto (estaciones 6 a 11), se observa una estratificación de las isotermas más o menos bien diferenciada desde la superficie hasta el nivel máximo muestreado. Aparentemente la isoterma de los 21.0°C no corta la superficie, dando como resultado que los valores superficiales sean mayores al valor menionado. En la estación 11 se presentó en la superficie el máximo valor de temperatura encontrado en toda la Bahia (más de 22.) C). El mínimo valor de temperatura, dado por la isoterma de los 15.0 C se localizó en la estación 9 a 50 m de profundidad.

En el transecto siguiente que comprende las estaciones 5 y 12 a 17, se observa que la termoclina está representada aparentemente por las isotermas de los 16.0 a 20.0°C, y que ésta se encuentra aproximadamente entre los 18 y 45 m de profundidad. La capa de mezcla tiene una profundidad promedio de 18 m. La isoterma de los 21.0°C corta a la superficie y por lo tanto solamente las estaciones 16 y 17 muestran valores menores de 21.0°C. La mínima temperatura se presentó a los 50 m en la estación 16 (menos de 15.0°C).

Para el útimo transecto (estaciones 4 y 18 a 22), la profundidad de la capa de mezcla para las estaciones 4 y 18 se presenta a 12 m. Para el resto de las estaciones presenta una mayor profundidad (aproximadamente 22 m). Aparentemente la termoclina está representada también por las isotermas de los 16.0 a 20.0 C, y se encuentra a una profundidad entre 22 y 45 m. Hacia la parte sur de la Bahia (estaciones 4 y 18, Figura 1) la termoclina sufre un desplazamiento hacia la superficie, acercándose a los 10 m. Para este transecto solamente las estaciones 20, 21 y 22 mostraron valores superficiales mayores de 21.0 C. A los 50 m de profundidad casi todas las estaciones presentaron valores menores de 16.0°C, excepto la estación 21 que a dicha profundidad tuvo un valor de 16.03 C. No se presentaron surgencias en ninguno de los tres transectos anteriores, según lo demuestra la distribución de las isotermas.

Salinidad

En los perfiles de la Figura 3, la distribución de salinidad es un tanto complicada sobre todo en el segundo transecto (estaciones 5 y 12 a 17). No se observa en ellos una haloclina bien definida, tampoco evidencias de surgencias. Los valores superficiales de salinidad son variables. La isohalina de los 35.5 °/oo (máximo valor de salinidad en estros transectos) se localiza en forma de nodos, observándose éstos tanto en la estación 9 a 10 m
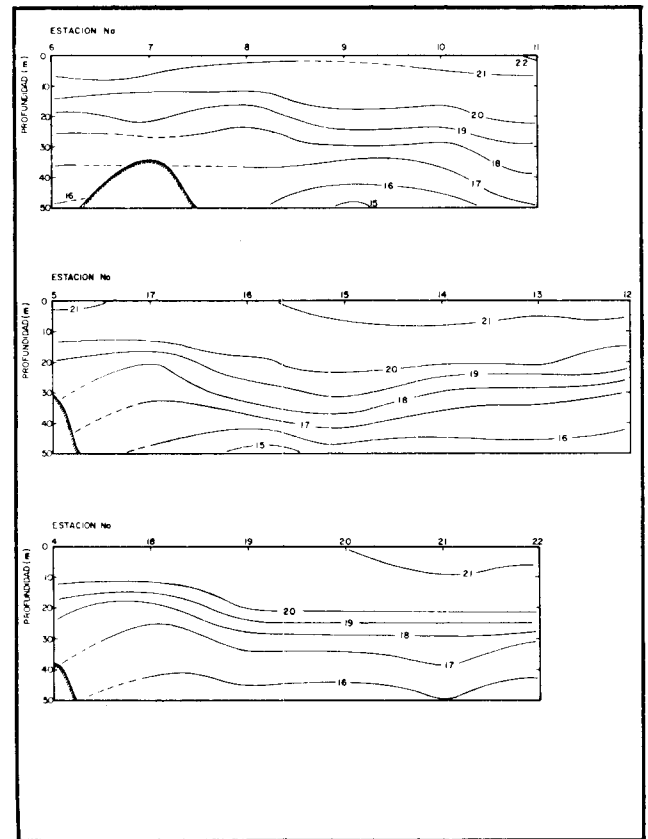
Figura 2. Gráficas de distribución vertical de temperatura (C). Intervalo de los contornos: 1.0 C. Crucero QM-7601, Abril de 1976.

de profundidad, como en la estación 15 a una profundidad de 30 m. El mínimo valor de salinidad representado por la isohalina de los 34.9 °/oo, se localiza entre los 30 y 40 m en la estación 4. Esta sugiere una intrusión hacia el norte que parece provenir junto con las isohalinas de los 35.0 y 35.1 °/oo de la parte sur de la Bahia.

Oxigeno Disuelto

Las gráficas de la Figura 4 muestran valores altos de oxigeno hasta una profundidad aproximada de 20 m. Para los tres transectos, la distribución y profundidad de la isolínea de los 5.0 ml/litro concuerda aproximadamente con la distribución y profundidad de la isoterma de los 20.0 C (Figura 2). Para el primer transecto (estaciones 6 a 11), la distribución del oxigeno se presenta más o menos estratificada, disminuyendo los valores conforme aumenta la profundidad. Para el segundo transecto correspondiente a las estaciones 5 y 12 a 17, la distribución de las isolineas de los 3.0, 4.0 y 5.0 ml/litro, corresponde más o menos con la distribución y profundidad de la termoclina para el mismo transecto (Figura 2). En el último transecto representado por las estaciones 4 y 18 a 22, la distribución de las isolineas de los 3.0 y 4.0 ml/litro, tienen un parecido con la distribució ye orientación de las isohalinas de los 34.9 a 35.1 °/oo que se
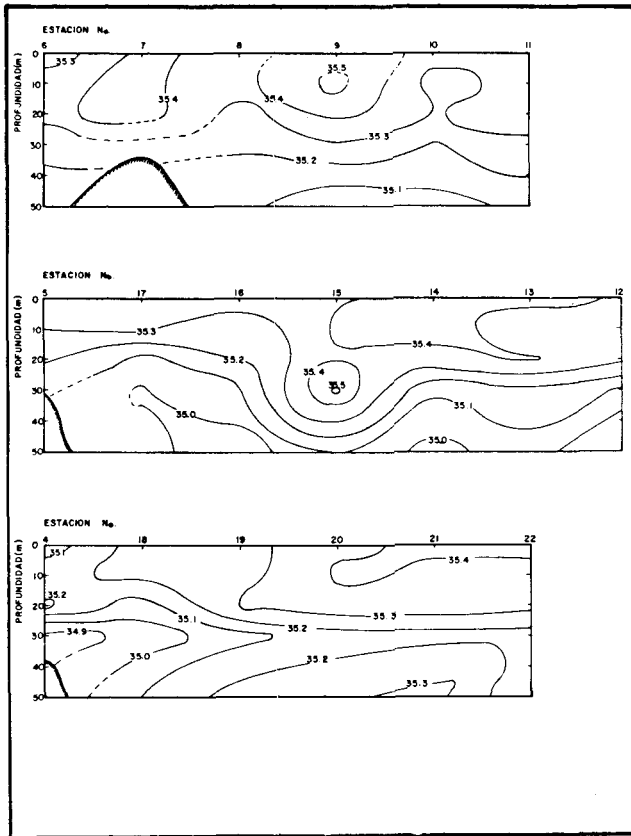
Figura 3. Gráficas de distribución vertical de salinidad (°/oo). Intervalo de los contornos: 0.1 °/oo. Crucero QM-7601, Abril de 1976.
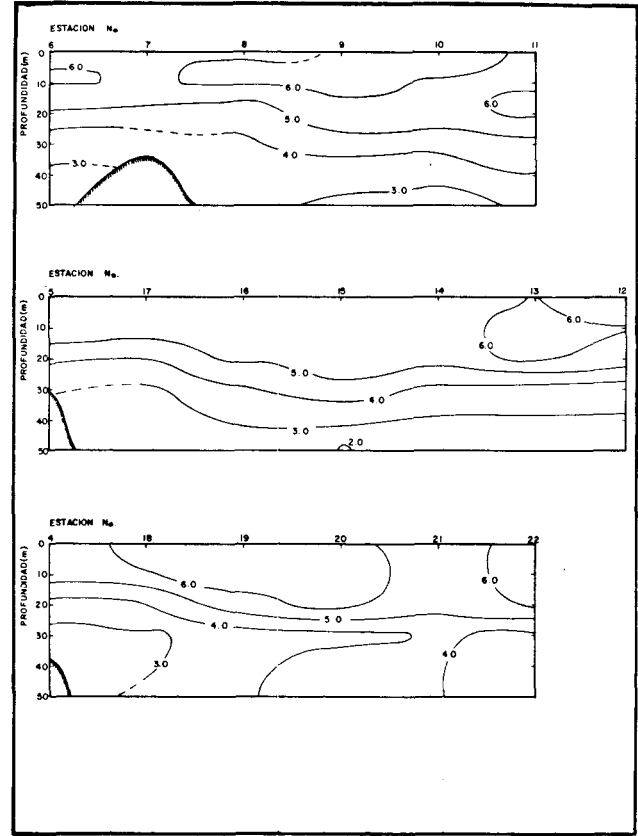
Figura 4. Gráficas de distribución vertical de oxigeno disuelto (ml/litro). Intervalo de los contornos: 1.0 ml/litro. Crucero QM-7601, Abril de 1976.

presentan en el mismo transecto (Figura 3).

El mínimo valor que se encontró de 2.0 ml/litro para todos los niveles muestreados, se localizó en la estación 15 a una profundidad de 50 m. Este mismo transecto parece mostrar evidencias de oxiclina.

DISCUSION

Los datos hidrográficos con que se cuenta para la Bahía de La Paz, Baja California Sur, son relativamente pocos. Por lo tanto las discusiones que pueden obtenerse a partir de ellos son necesariamente limitadas y solo deben tomarse como una primera aproximación hasta que se cuente con más datos en trabajos futuros.

En el presente estudio se encontró que la distribución vertical de las propiedades en la Bahía parecen estar íntimamente ligados con los fenómenos atmosféricos. La profundidad de la capa de mezcla que fue más notoria en el segundo y tercer transecto de la Figura 2, se sugiere que es el resultado de la intensidad y duración del viento como lo demuestran los valores en la Tabla 1. En ella se muestra que dichos valores son menores en las estaciones del primer transecto que para los dos restantes. Cuando estos valores fueron bajos la distribución de la temperatura se presentó en una forma más o menos estratificada,

mientras que en el segundo y tercer transecto donde se observa la capa de mezcla, corresponden precisamente a aquellas estaciones donde la velocidad del viento fue mayor.Es difícil saber con certeza cuales isotermas son las componentes de la termoclina por la relativamente poca profundidad a que fué hecho el estudio. Sin embargo, el espesor y la profundidad de la termoclina encontrados en el presente trabajo concuerdan aparentemente con los resultados obtenidos por otros investigadores. Dichas investigaciones se realizaron en la entrada del Golfo de California durante la misma estación del año (Griffiths 1968; Roden y Groves 1959).

Por lo que respecta a salinidad, se encontró que el agua muestreada en la Bahía pertenece a agua superficial del Golfo de California. Según Griffiths (1968) dicha agua presenta salinidades mayores de 35.0 °/oo debido a la fuerte evaporación que se lleva a cabo en las aguas superfciales del Golfo. Se encontraron valores mayores de 35.0 °/oo (Figura 3), exceptuando en el tercer transecto el valor de la isohalina que forma la pequeña instrusión de 34.9 °/oo que parece provenir de la parte sur. Aún así, esta isohalina también pertenese al agua superficial del Golfo, pues Roden y Graves (1959) mencionan que dicha agua presenta valores de salinidad desde los 34.8

TABLA 1

Velocidad y Dirección del Viento en las Estaciones Ocupadas durante el Desarrollo del Crucero QM-7601.

Numero de Estacion	Fecha (abril, 1976)	Hora (local)	Viento Velocidad (m/seg)	Viento Dirección
1	25	07:55	1.0	SE
2	25	08:55	1.5	SE
3	25	09:51	1.0	SE
4	25	10:55	0.0	–
5	25	11:39	0.5	SE
6	25	13:02	0.5	SE
7	25	14:16	1.0	NNW
8	25	15:38	1.5	SSE
9	25	16:40	1.5	SSW
10	25	17:40	2.6	WSW
11	25	18:39	1.0	SE
12	25	20.07	2.6	SSW
13	25	21:07	6.7	SW
14	25	22:11	6.7	SSW
15	25	23:29	10.3	SSW
16	26	07:45	6.2	SSE
17	26	09:06	5.2	SSE
18	26	09:56	8.2	SSE
19	26	10:55	6.2	SSE
20	26	11:50	3.6	SSE
21	26	13:06	2.6	SSE
22	26	14:02	5.7	SSE
23	26	15:18	7.7	ENE
24	26	16:42	4.6	S

^{o}/oo. Probablemente debido a la gran turbulencia producida por los fuertes vientos del SSE que estuvieron soplando ocasionó que no estuviera bien representada la haloclina, excepto en el segundo transecto donde parece presentarse (Figura 2). Este mismo fenómeno probablemente también originó los pequeños nodos con valores altos de salinidad encontrados en las capas subsuperficiales junto con la distribución un tanto complicada de las isohalinas.

La distribución vertical de las isotermas y las isohalinas no presentaron surgencias en ninguna parte de la Bahia. Entre otros complicados procesos, las surgencias son inducidas por la dirección del viento, por la intensidad y por su duración, asi como por la morfologia de las costas (Roden 1958). Con vientos del sur solamente se presentan surgencias en la costa oeste del Golfo de California a sotavento de cabos, islas y puntas como son: norte de Bahia Concepción, en la zona comprendida entre las Islas Carmen, Santa Catalina, Santa Cruz y San José, y en la vecindad de la Isla Cerralbo (Roden 1958, 1959; Groves y Reid 1958; Roden y Groves 1959).

En la distribución vertical de oxigeno (Figura 4), los altos valores de más de 5.0 ml/litro se localizaron hasta una profundidad aproximada de 20 m. Dicha profundidad corresponde aproximadamente con la capa de mezcla. La profundidad y distribución de la isolinea de los 5.0 ml/litro es consistente con la capa de mezcla obtenida en las gráficas de distribución vertical de temperatura (Figura 2). Los altos valores encontrados se debieron a oxí-

genación de las capas superficiales. Esta fué producida por la turbulencia provocada por los fuertes vientos que se presentaron durante el crucero, principalmente cuando se ocuparon las estaciones del segundo y tercer transecto. Este mismo fenómeno dió como resultado la aparente ausencia de oxiclina, excepto en el segundo transecto donde hay evidencias de ella.

Se encontraron intrusiones con valores relativamente bajos de salinidad y oxigeno disuelto, las cuales se presentaron en la parte sur del transecto más cercano al Canal de San Lorenzo. Tentativamente se sugiere que dichos valores se debieron a la mezcla producida por las corrientes que se originan en el canal mencionado. Más tarde, probablemente los vientos indujeron las capas subsuperficiales de la Bahia hacia el norte.

Es necesario conocer la variación estacional de los parámetros hidrográficos en la Bahia de La Paz a través de todo un ciclo anual y además muestrear toda la columna de agua hasta el fondo. En el presente estudio no se pudieron ocupar las estaciones que se encontraron en aguas circunvecinas al Canal de San Lorenzo, obteniéndose con lo anterior que no se pudiera conocer la influencia que dicho canal tiene sobre la Bahia.

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RESULTADOS PRELIMINARES SOBRE LA DISTRIBUCION SUPERFICIAL DE PARAMETROS FISICO-QUIMICOS EN LA ENSENADA DE LA PAZ, BAJA CALIFORNIA SUR, DURANTE LA PRIMAVERA DE 1976

JULIO ESPINOZA-AVALOS
Centro de Investigaciones Biológicas, A.C.
La Paz, Baja California Sur
Mexico

ABSTRACT

The results of hydrographic measurements during two surface samplings in the Ensenada de La Paz, on 6 May 1976 during high and low tides are presented. Two zones differentiated by sediments and depths were evident: a southern region with shallow depth and muddy bottom with high temperature and salinity, poor transparency, and low oxygen and a northern region with opposite conditions.

Temperature, salinity, dissolved oxygen, and transparency were found to be higher during high tide in the afternoon than during low tide in the morning. The influence of the chemical and physical characteristics of the outer waters of the Bahía de La Paz, which have greater transparency, higher dissolved oxygen, and lower temperature and salinity than the waters of the Ensenada was noted. This was clearly detected during the incoming tide at the mouth of the Ensenada de La Paz.

RESUMEN

Se presentan los resultados de las mediciones hidrográficas durante dos muestros superficiales realizados el día 6 de mayo 1976, en marea alta y marea baja. La Ensenada de la Paz presentó una diferenciación de dos zonas debido a la batimetria y a tipos de sedimentos existentes; una hacia el sur de la Ensenada, con poca profundidad y sedimento fangoso, lo cual hace que la temperatura y la salinidad sean mayores y la transparencia y el oxígeno disuelto sean menores, sucediendo lo contrario en la parte norte.

La temperatura, salinidad, oxígeno disuelto y transparencia, fueron mayores en marea alta por la tarde que en marea baja por la mañana. Se observó la influencia de las características hidrológicas de la Bahía de La Paz, la cual presenta mayor transparencia y concentración de oxígeno disuelto y menor temperatura y concentración de salinidad que la Ensenada de La Paz. Se observó esto más claramente en la entrada de la Ensenada, durante la pleamar.

INTRODUCCION

Los resultados que aquí se presentan forman parte de un estudio hidrográfico de la Ensenada de La Paz (Figura 1) que comprende muestreos sistemáticos durante un ciclo anual que se realizarán durante cada estación del año, habiéndose iniciado en la primavera de 1976.

El día 6 de mayo de 1976, se realizaron dos muestros superficiales; uno en marea baja y otro en marea alta, con el objeto de observar las variaciones en las características físico-químicas del agua de mar después de haber permanecido durante el período de tiempo existente en un ciclo de marea y en cuyo lapso ocurren cambios en las propiedades. Las horas de los muestreos se presentan en la Figura 2, cubriéndose el plan de estaciones que se muestran en la Figura 1.

La región que circunda a la Ensenada es una planicie que presenta un declive muy leve hacia el mar y está constituida por sedimentos aluviales. Está separada de la Bahía por una barra de arena denominada "El Mogote," y solo se comunica con ella por medio de un canal que mide aproximadamente 1 km de ancho. El Mogote mide alrededor de 11 km en sentido este-oeste y aproximadamente 2.7 km en su parte más amplia y está cubierto de arbustos y plantas halófitas (Holguín 1971). En su litoral existen entradas de agua de mar someras que a veces forman canales estrechos con profundidades hasta de dos metros durante marea alta y en las cuales abunda vegetación de manglares (Figura 1).

La profundidad máxima de la Ensenada no excede los 10 m en sus partes más profundas (Figura 3). Se presentan en un canal central desde la boca, el cual se prolonga hasta el interior de la Ensenada. Dentro de ella existen grandes zonas de entremareas con pendientes a veces imperceptibles, sobre todo en la parte sur.

Félix-Pico (1975) reporta el tipo de sedimentos que se encuentran en la Ensenada, y en ella se observan grandes zonas de fango y detritus (Figura 4), sobre todo en las partes más someras del litoral sur, donde desembocan las descargas de aguas municipales. La Dirección de Hidrología de la S.R.H. (Félix-Pico 1975) reporta una evaporación promedio anual de 215 mm y una precipitación promedio anual de 180 mm (siendo septiembre el mes más lluvioso). La humedad relativa anual varía del 66 al 72%, lo que hace que esta zona sea seca o desértica.

Los vientos dominantes de noviembre a marzo provienen del noroeste y se les llama localmente "Collas," de abril-agosto, circulan con dirección oeste-sureste y son conocidos como "Coromueles," también existe la influencia de ciclones tropicales durante los meses más lluviosos.

En cada estación se determinó la temperatura, pH, y transparencia del agua, y se tomaron muestras de agua para analizar oxígeno disuelto y salinidad. Se obtuvo
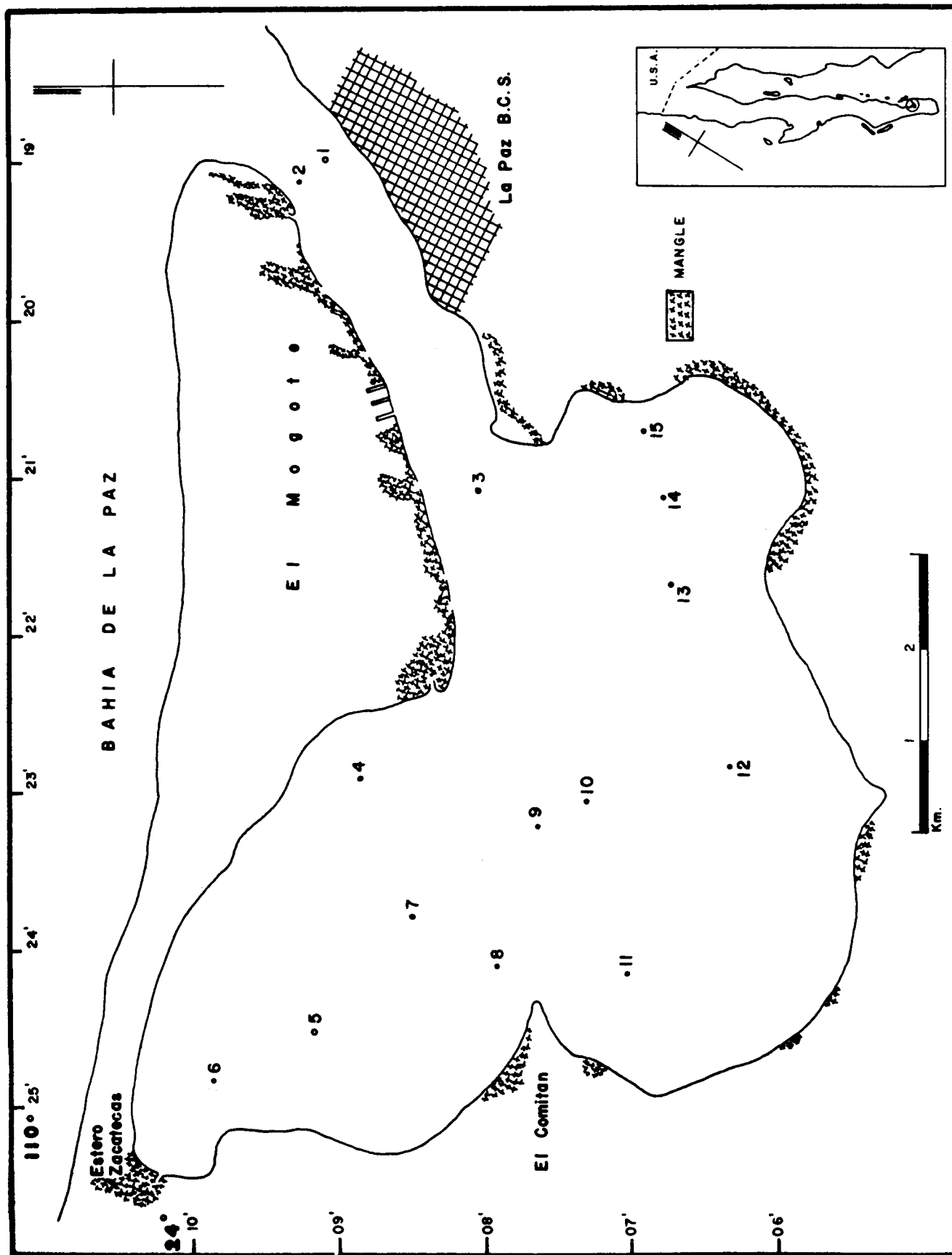
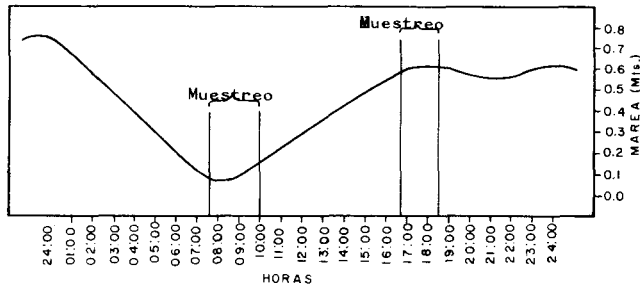Figura 1. Localización de las estaciones de muestreo.

Figura 2. Gráfica de marea indicando las horas de muestreo, el 6 de mayo en la Ensenada de La Paz.

también el porciento de saturación del oxígeno y se tomaron además datos meterológicos. Los métodos que se utilizaron para la obtención de los datos fueron los tradicionales.

RESULTADOS Y DISCUSIONES

En este trabajo solo se discutirán los valores obtenidos de temperatura, salinidad, oxígeno disuelto y transparencia del agua.

Temperatura

Los resultados de temperatura en bajamar y pleamar se presentan en las Figuras 5 y 6 respectivamente. Se observa que los valores fueron mayores por la tarde durante la pleamar, debido a la mayor incidencia de radiación solar a que había sido expuesta la superficie de la Ensenada. El incremento en la temperatura es mayor en las zonas someras, sobre todo en la parte sur de la Ensenada, donde existe una gran zona de entremareas. Lo anterior pone de manifiesto la influencia de la radiación solar en la variación de la temperatura con el tiempo, asimismo la influencia de la batrimetría en la distribución superficial de este parámetro.

Los valores mínimos para bajamar y pleamar fueron de 19.1°C y 21.6°C occuridos en las estaciones 4 y 2 los máximos de 22.2°C y 23.7°C, ambos presentados en la estación 15 (Figura 1). El rango de temperatura fué mayor en marea baja (3.1°C) que en marea alta (2.1°C). En ambos extremos de nivel de marea, los valores menores presentados en la entrada de la Ensenada hacen notar la influencia del agua más fria de la Bahía. Villaseñor (1976) reporta valores en la Bahía de 20.75°C a 21.00°C cerca de la entrada de la Ensenada (a 0 y 10 m de profundidad.) Dichos valores concuerdan más con los valores encontrados en marea baja debido a que los muestreos en la Bahía, en las estaciones cercanas a la boca de la Ensenada también se realizaron por la mañana.

Salinidad

La distribución de salinidad en bajamar y pleamar se

presentan en las Figuras 7 y 8 respectivamente. Igual que en la distribución de temperatura, los valores mínimos se presentaron en general en la entrada y los máximos hacia el sur de la Ensenada. En la parte norte, donde existe la zona de más profundidad se observa en marea alta mayor homogeneidad en las valores. Lo anterior sugiere la influencia de la batrimetría en la distribución de salinidad. En bajamar los valores extremos fueron 36.42 °/oo y 38.17 °/oo (estación 4 y 14) y en pleamar 35.43 °/oo y 38.83 °/oo, ocurridos en las estaciones 2 y 15 (Figura 1). El rango fue mayor en marea alta, 3.39 °/oo, en comparación con bajamar que fue de 1.75 °/oo. Los valores reportados por Villaseñor (1976) para la Bahía de La Paz, cerca de la entrada a la Ensenada, son de 35.30 °/oo y 35.40 °/oo a 0 y 10 m de profundidad. Estos datos concuerdan con los valores de salinidad encontrados en marea alta, los cuales fueron de 35.50 °/oo en la entrada del canal. Para marea baja los datos de salinidad en la entrada de la Ensenada no concuerdan con los datos de la Bahía, debido a que en ese nivel de marea la influencia es del interior de la Ensenada, donde existen valores mayores a los del exterior. Se observa así la influencia de la marea en la distribución superficial de este parámetro.

En ambos niveles de marea se observa en general, que los valores de salinidad aumentan desde la entrada hacia del interior de la Ensenada, donde existen valores mayores donde existe la gran zona de entremareas. Esto es debido a que la Ensenada funciona como una cuenca de evaporación.

Oxigeno Disuelto

Se presenta en las Figuras 9 y 10 la distribución de oxígeno disuelto en la Ensenada de La Paz. Comparando estas figuras, se observa que por la tarde en pleamar existen mayores concentraciones. Por la mañana en bajamar (Figura 9), los valores varían de 4.62 a 5.41 ml/litro (estaciones 11 y 15) y en pleamar varian de 5.28 a 6.26 ml/litro (estaciones 6 y 2, Figura 1). Los rangos fueron de 0.79 y 0.98 ml/litro respectivamente.

Posiblemente el fitoplancton sea el responsable de las altas concentraciones de oxígeno disuelto que se encontraron durante el muestreo que se realizó por la tarde. La radiación solar al estimular al fitoplancton durante el dia hizo que por medio de la fotosintesis, éste produjera el oxígeno disuelto. Es evidente la importancia del ciclo de radiación solar en la variación del oxígeno disuelto con el tiempo.

Villaseñor (1976) reporta valores de oxígeno disuelto de 5.25 ml/litro a 0 y 10 m de profundidad cerca de la entrada a la Ensenada. Estos concuerdan solo con los valores que se encontraron en marea baja. Probablemente esto se deba a que ambos muestreos se realizaron a
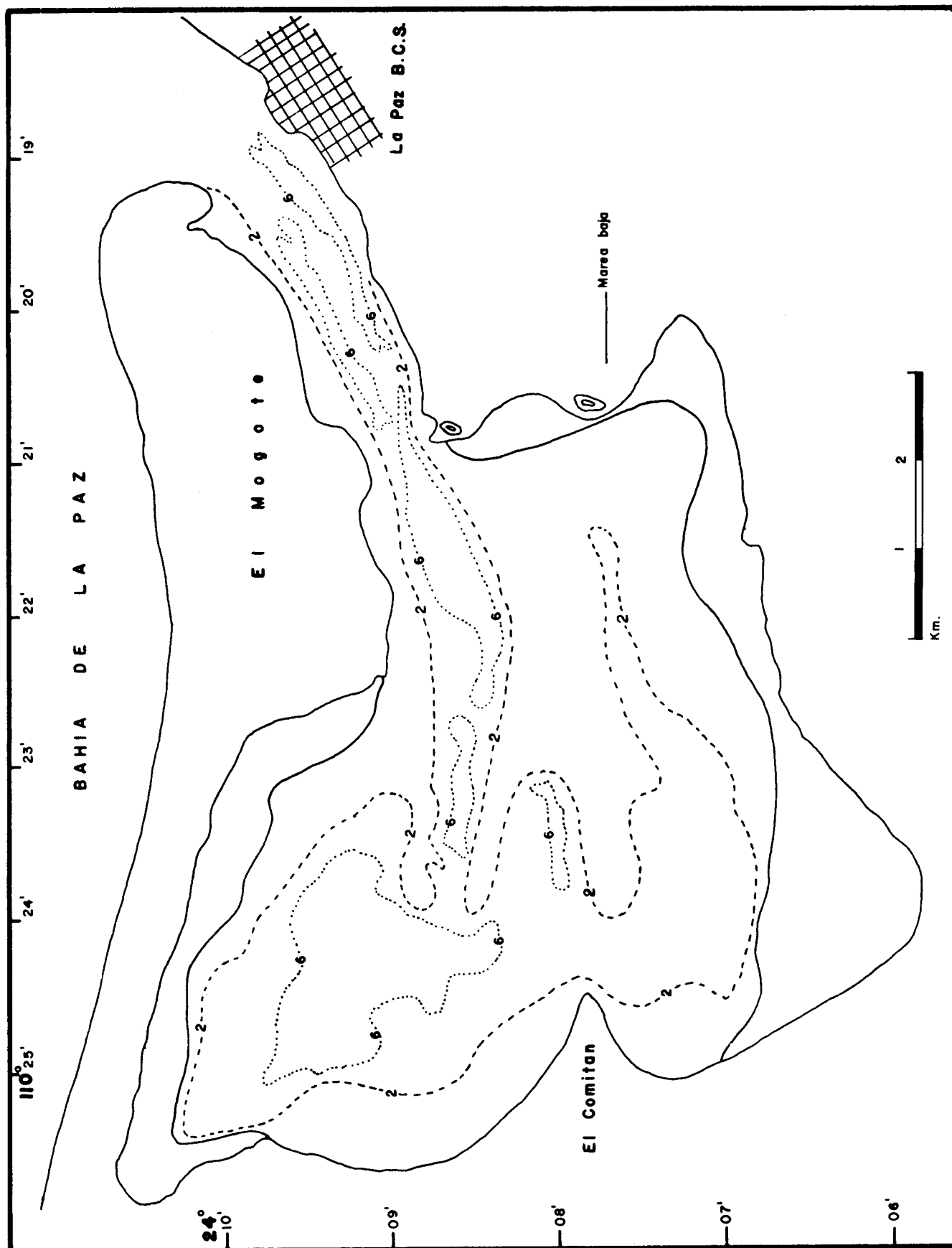
Figura 3. Batimetría de la Ensenada de La Paz (m).
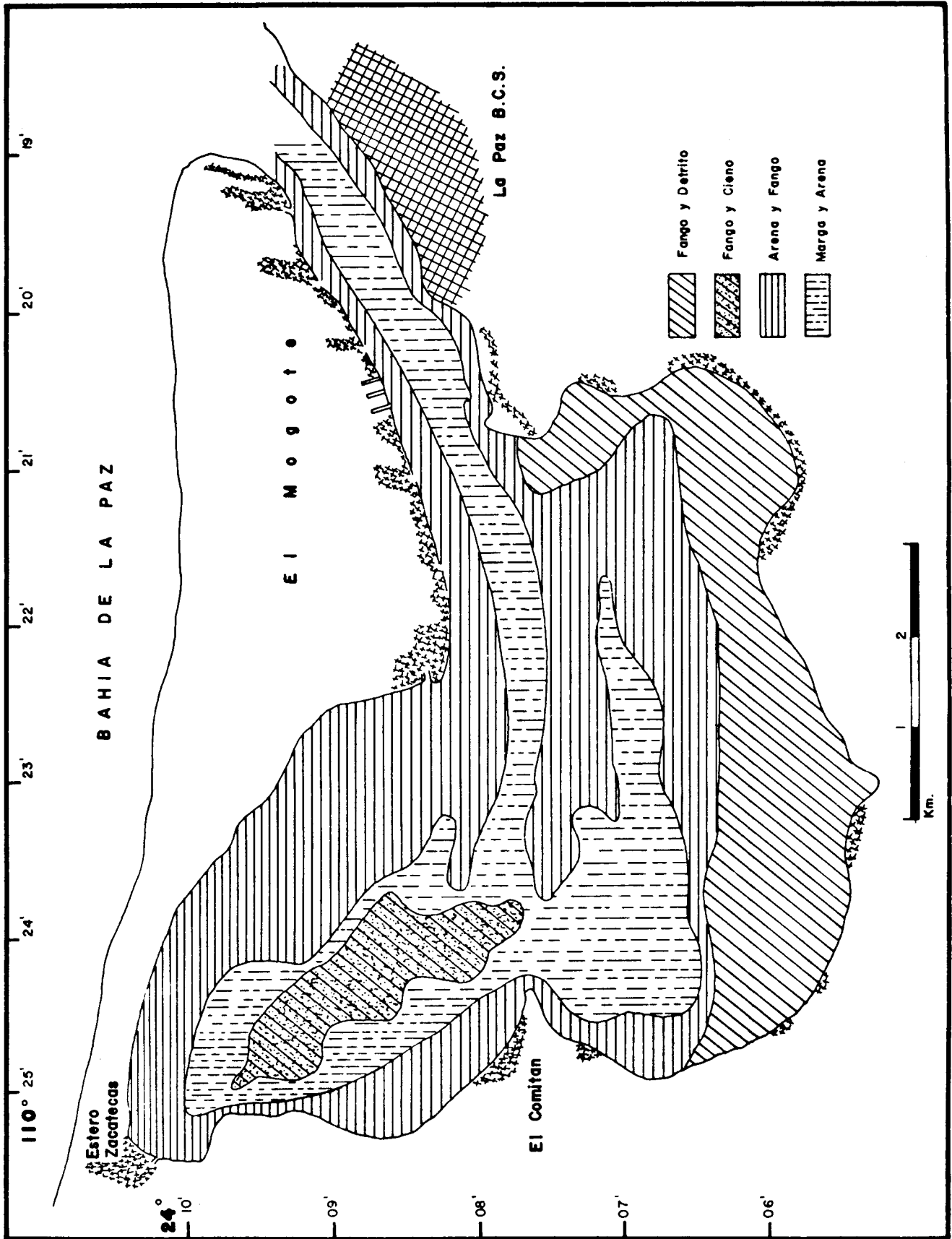
Figura 4. Distribución de tipos de sedimento durante el verano de 1975.
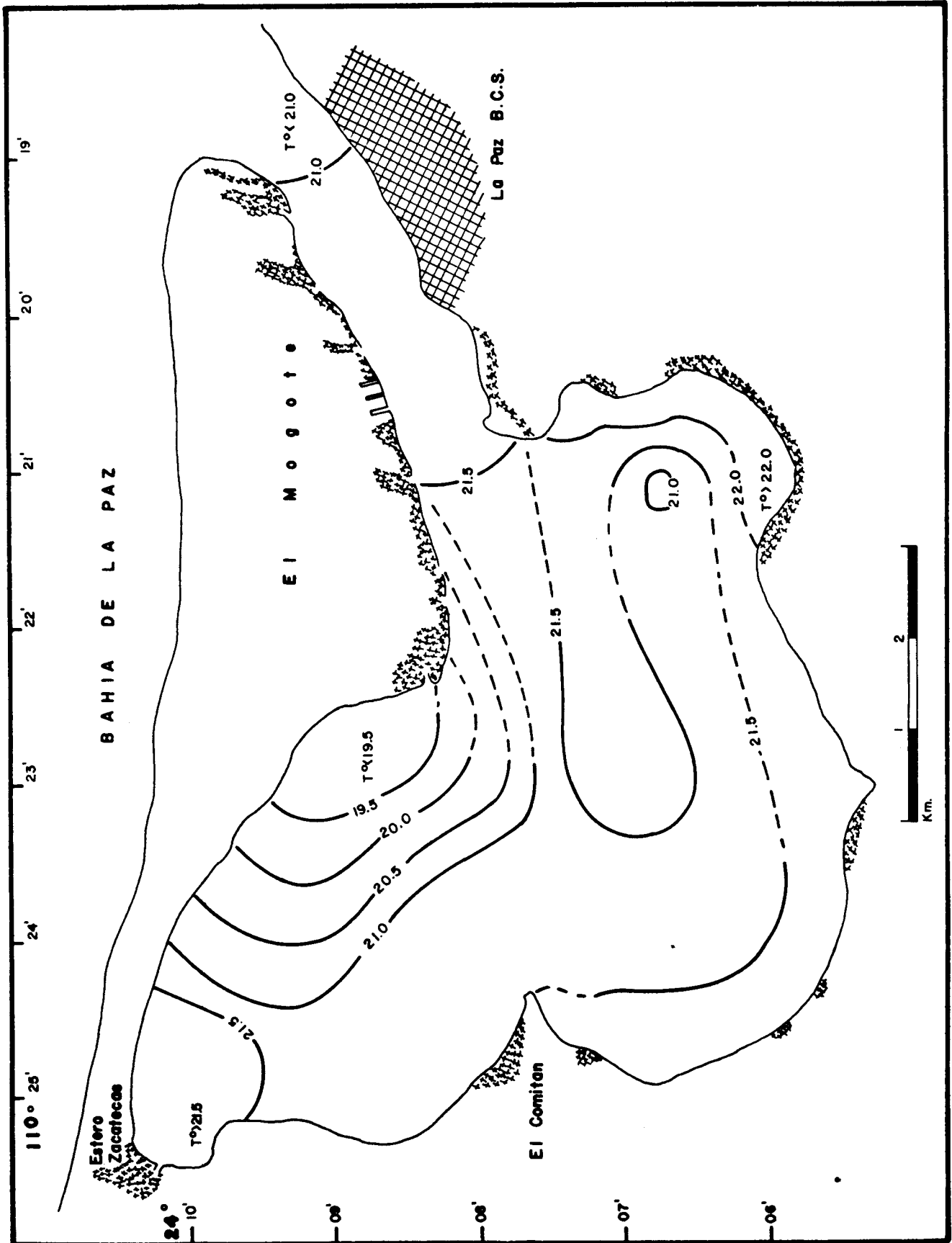
Figura 5. Distribución superficial de T C durante marea baja.
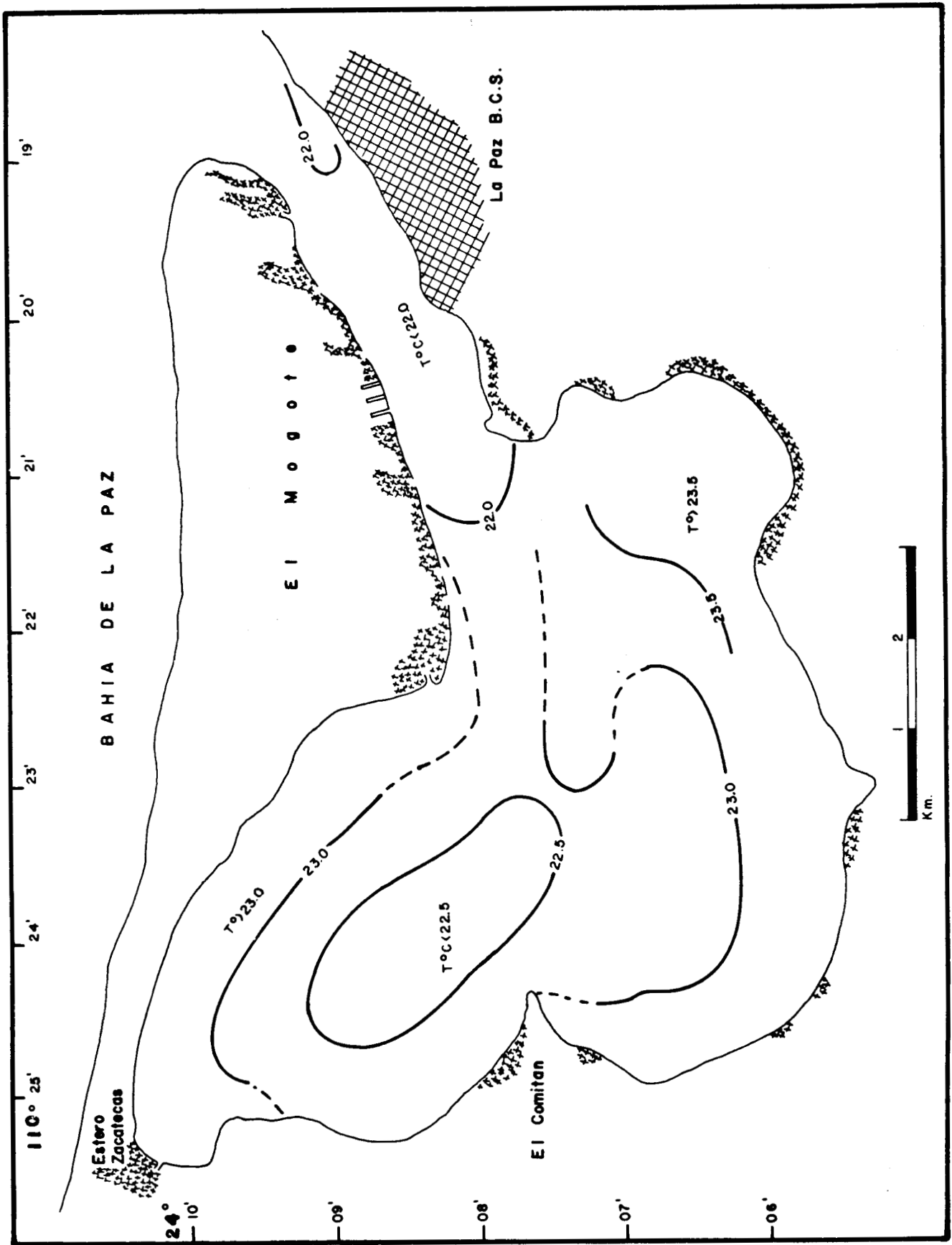
Figura 6. Distribución superficial de T C durante marea alta.
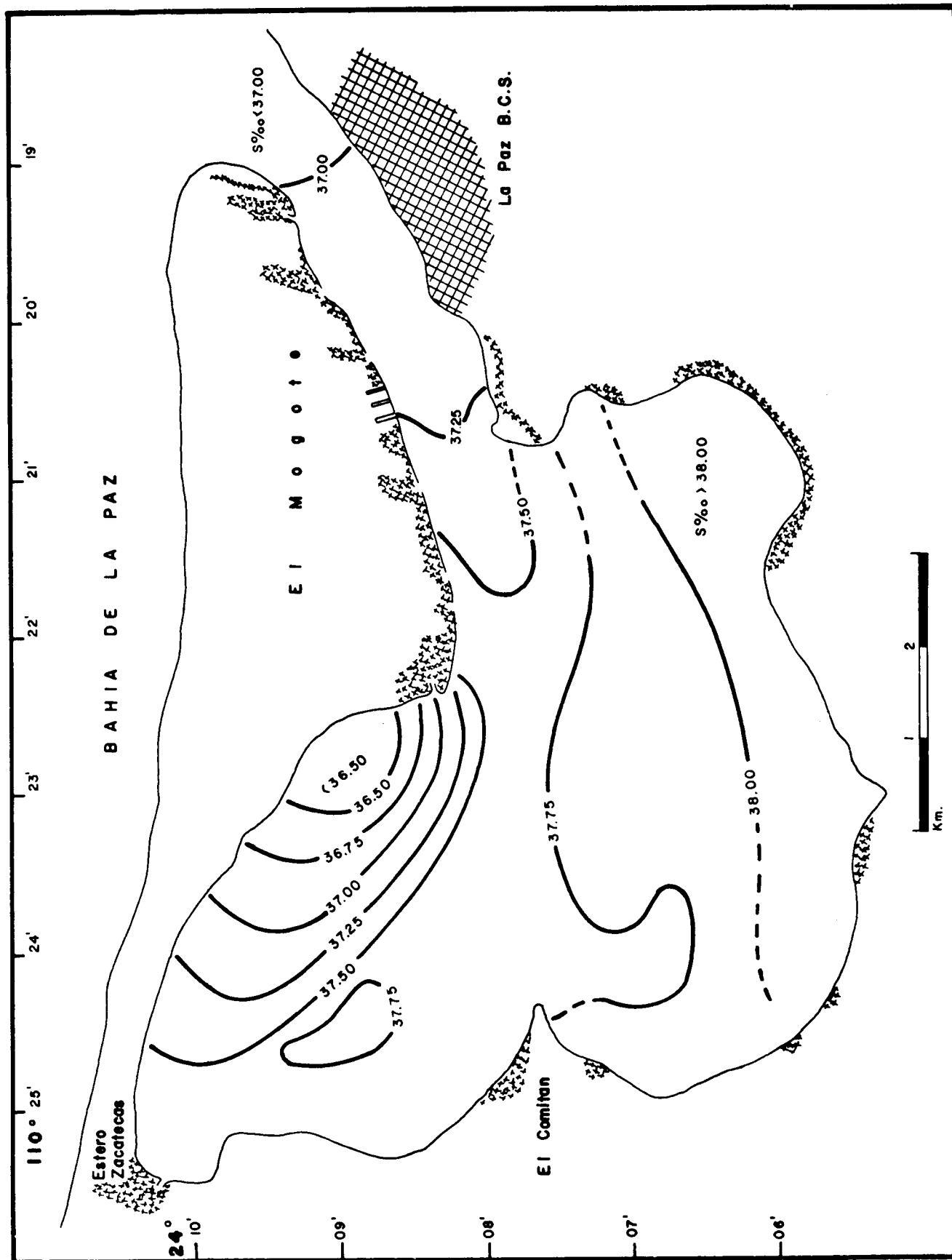
Figura 7. Distribución superficial de salinidad (S °/oo) durante marea baja.
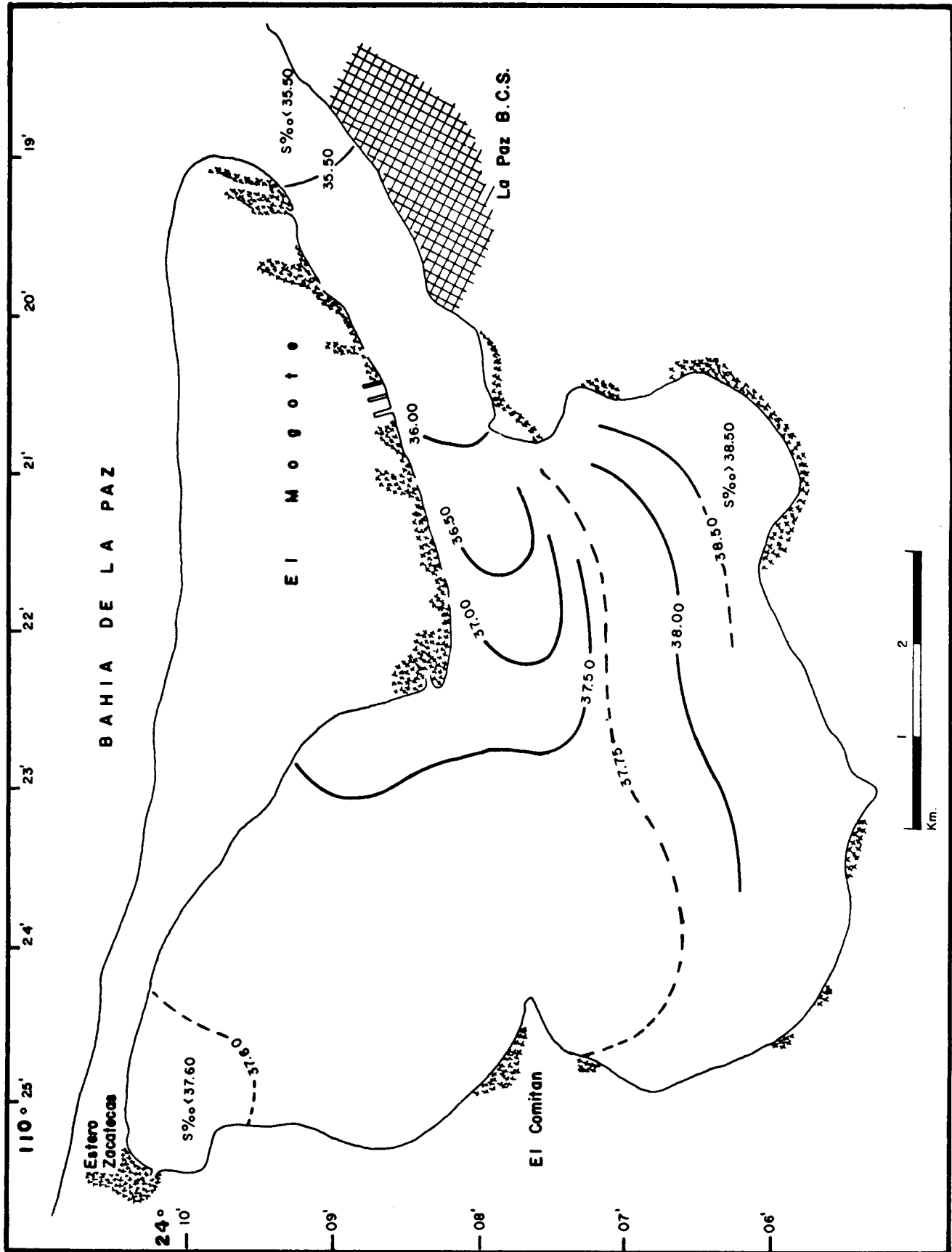
Figura 8. Distribución superficial de salinidad (S º/oo) durante marea alta.
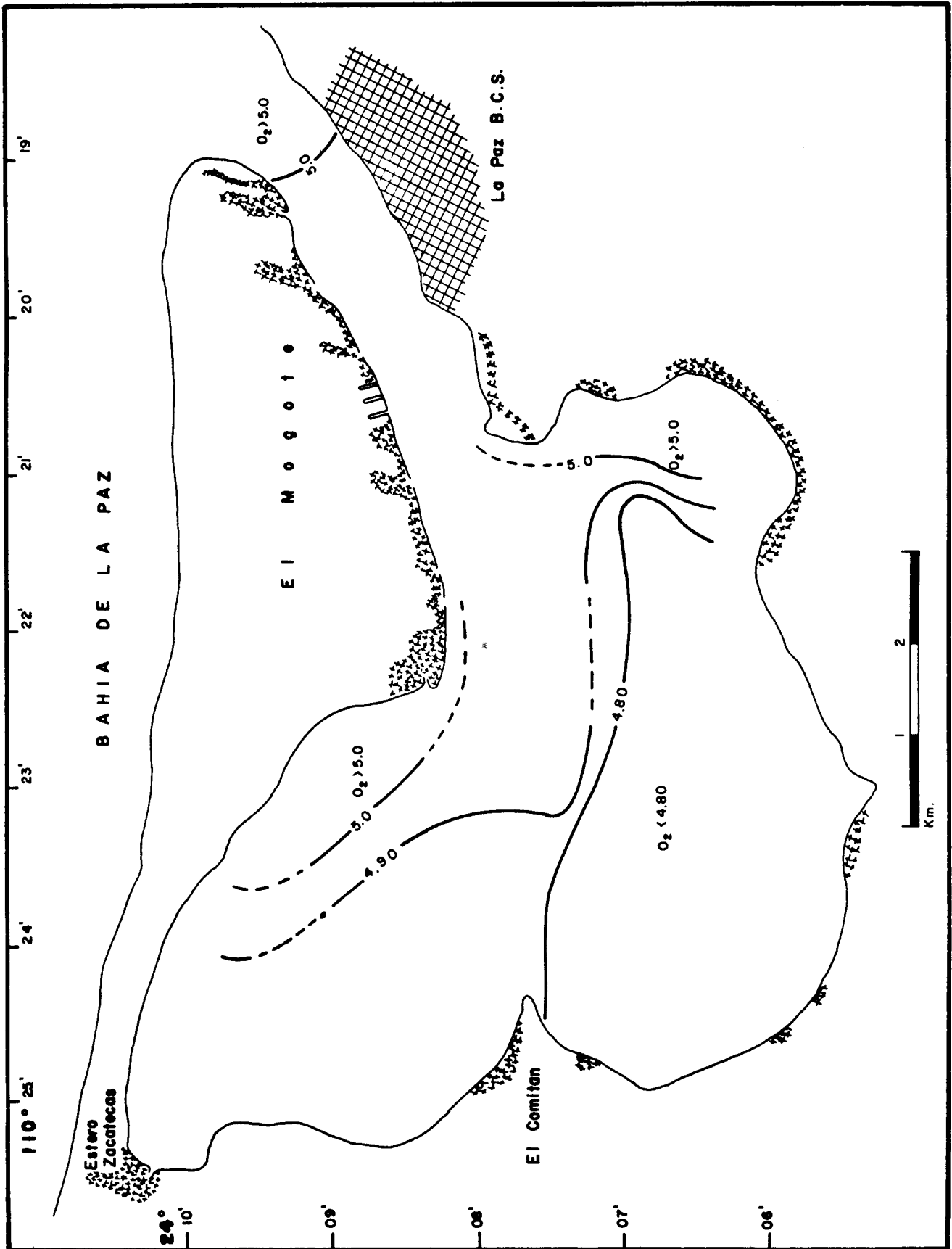
Figura 9. Distribución superficial de oxígeno (ml/litro) durante marea baja.
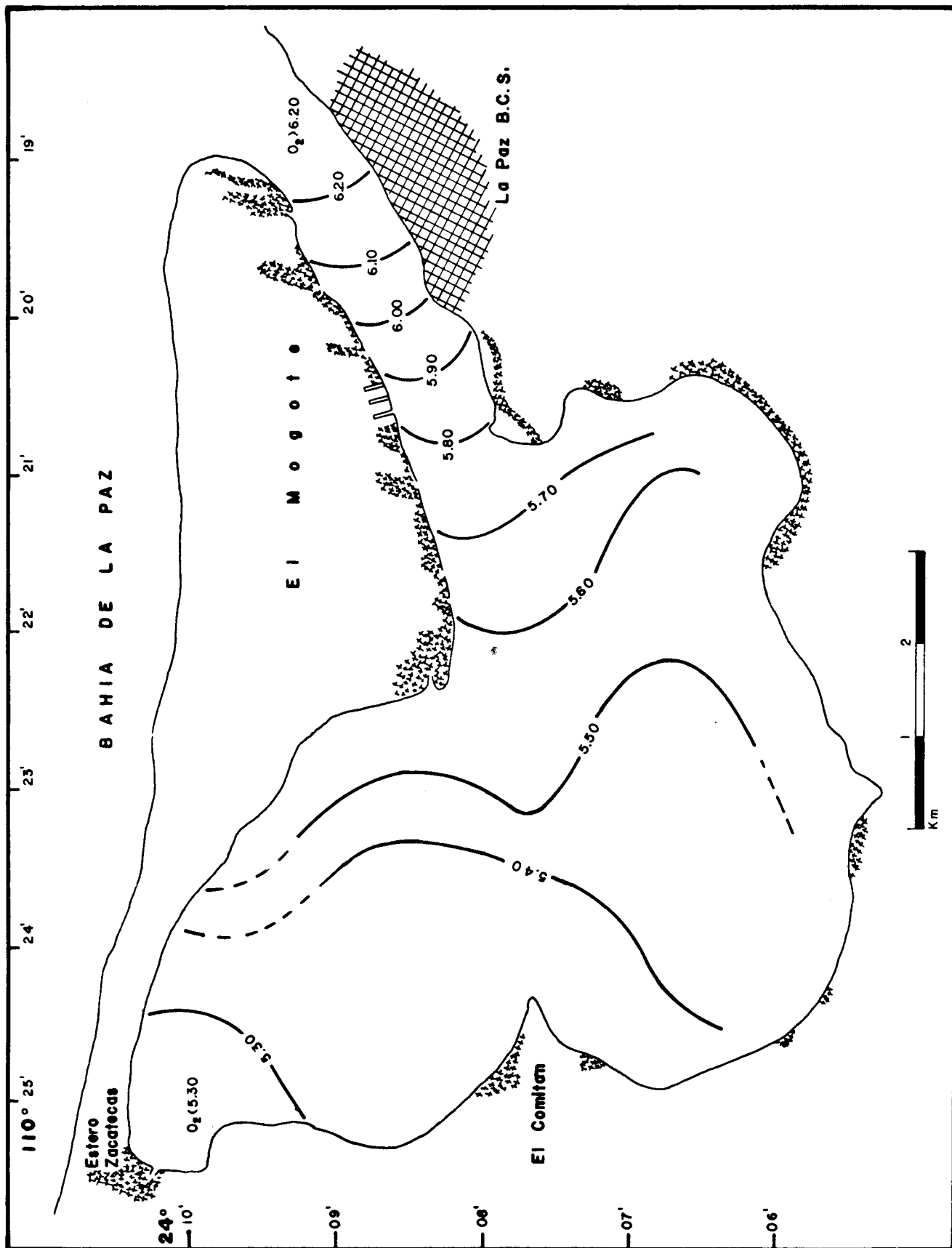
Figura 10. Distribución superficial de oxígeno (ml/litro) durante marea alta.

primeras horas de la mañana.

Solo en marea baja se presentaron valores de oxígeno disuelto que permiten diferenciar las zonas norte y sur con los valores mínimos hacia el sur de la Ensenada, que es la zona amplia de entremareas y con presencia de fango y además donde existen las descargas residuales municipales. Lo anterior en conjunto hace que en esta zona exista abundante materia orgánica en descomposición, con la consecuente disminución de oxígeno disuelto. Hacia la parte sur de la Ensenada donde se presenta la isolínea de los 4.80 ml/litro (Figura 9), se han reportado abundantes poblaciones de la almeja catarina, *Argopecten* sp. (Yoshida, comunicación personal), las cuales muy probablemente también contribuyeron a la disminución del oxígeno disuelto.

En marea alta (Figura 10), se presenta solo un gradiente que disminuye gradualmente desde la entrada de la Ensenada hasta el interior, cerca del Estero Zacatecas, sugiriendo esto la influencia que la marea produce en la distribución del oxígeno disuelto.

Transparencia

En la Figura 11 se presentan los resultados en marea baja y en la Figura 12 los de marea alta. Las mayores transparencias ocurrieron en marea alta cerca de la entrada a la Ensenada, alcanzando valores hasta de 5.0 m, los cuales se supone son debidos a la influencia de las aguas más transparentes de la Bahía. Villaseñor (comunicación personal), encontró valores de transparencia en la Bahía, de 9 a 10 m en las estaciones cercanas a la entrada y hasta de 19 m para otras. En bajamar, tanto en la entrada como en el canal, los valores son mayores, sin embargo estos son menores con respecto a pleamar debido a la influencia del sedimento que se encuentra en el interior de la Ensenada que por las corrientes de marea son acarreados en suspensión hacia el exterior. Dentro de la Ensenada se distinguen facilmente dos zonas; una con menor transparencia hacia el sur que es donde se presentan las amplias zonas de entremareas y la zona de fango (Figuras 3 y 4). La otra hacia la parte norte con mayores valores, donde inclusive se presentan núcleos que corresponden a las zonas de máxima profundidad. La distribución de transparencia sugiere la influencia de la batimetría y el sedimento en la Ensenada.

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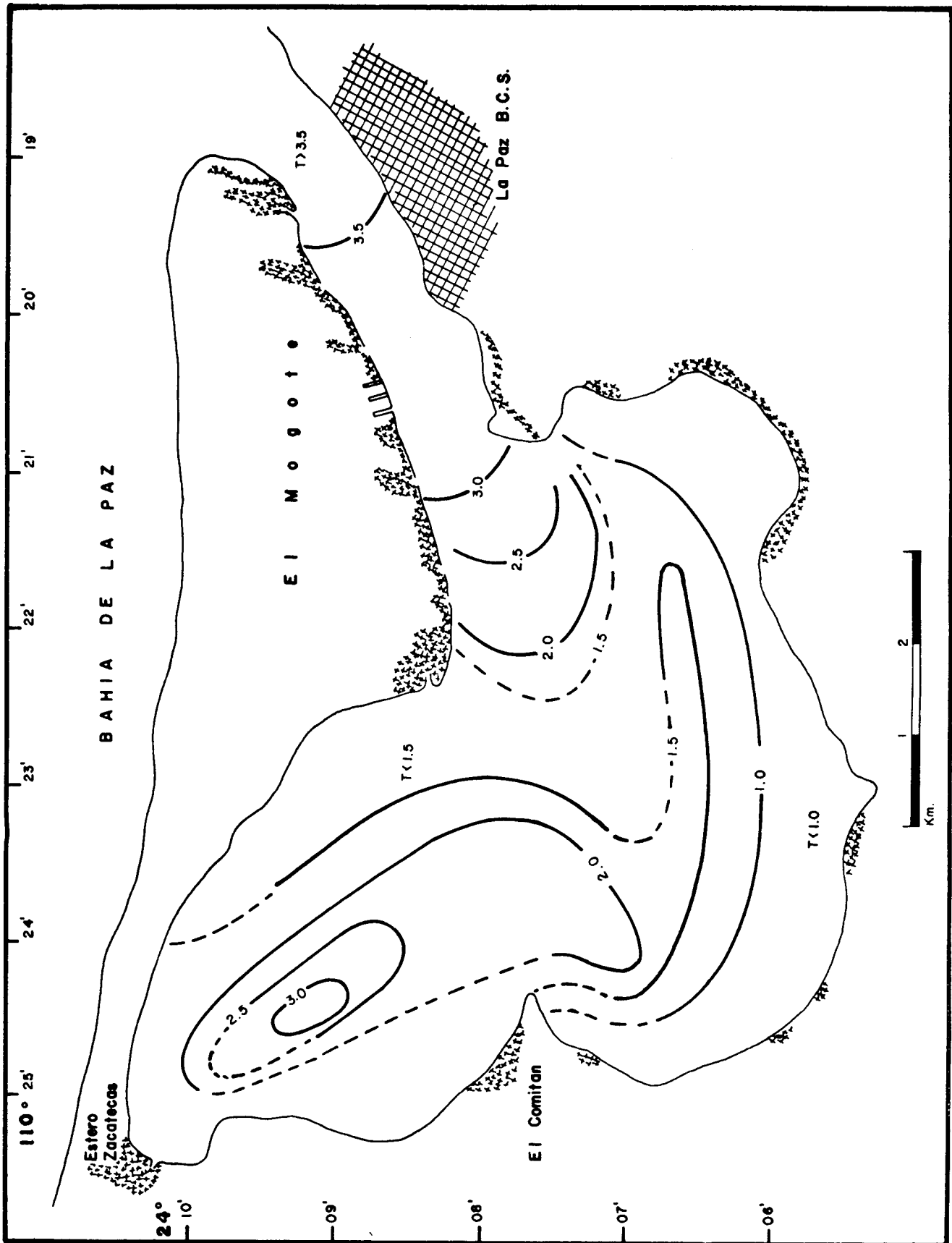
Figura 11. Distribución de transparencia (m) durante marea baja.
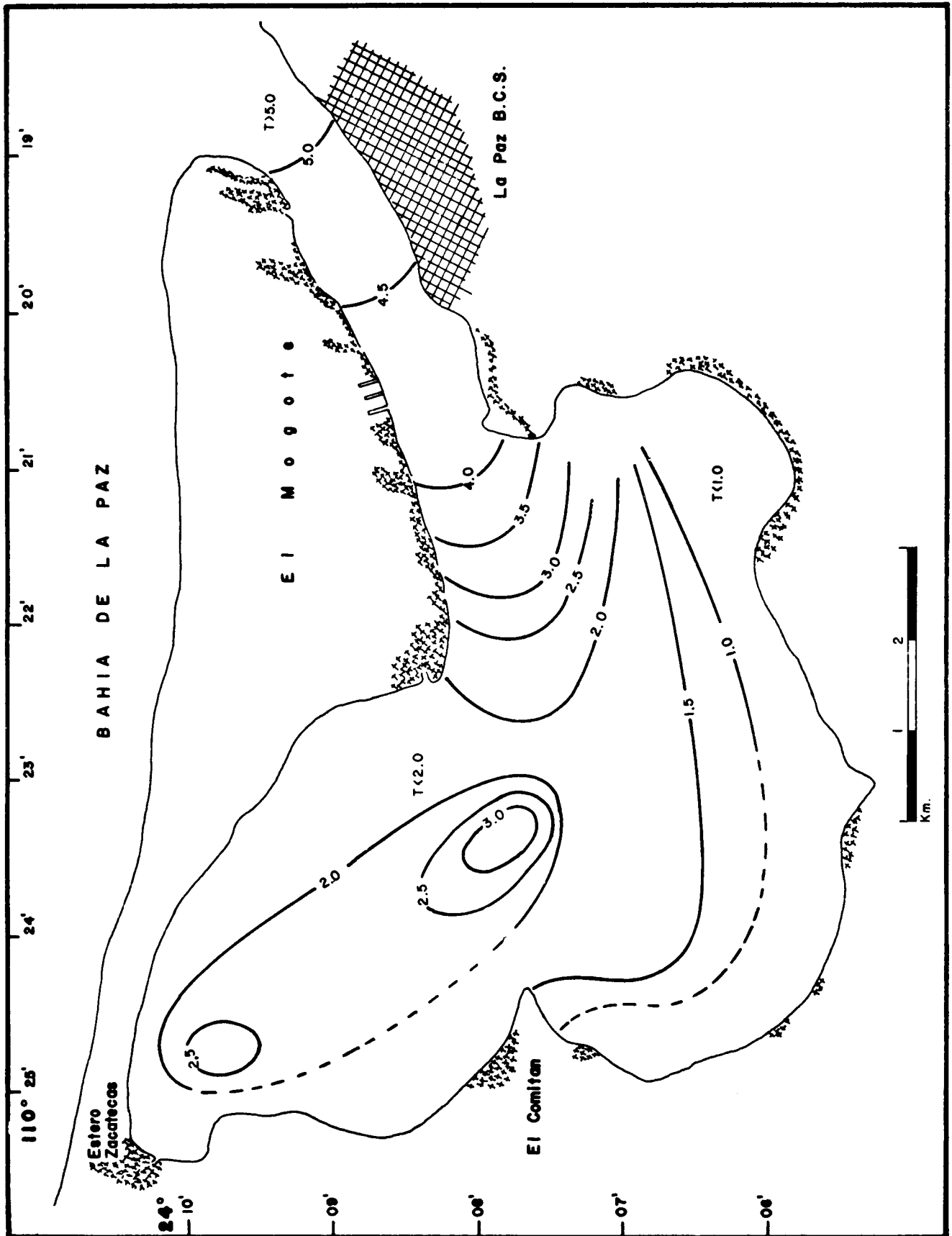
Figura 12. Distribución de transparencia (m) durante marea alta.

A DESCRIPTION OF THE CALIFORNIA CURRENT ECOSYSTEM BY FACTOR ANALYSIS

GEORGE T. HEMINGWAY
Scripps Institution of Oceanography
University of California San Diego
La Jolla. CA 92093

INTRODUCTION

The California Current has been studied extensively since the California Cooperative Oceanic Fisheries Investigations (CalCOFI) were begun in 1949. Monthly or quarterly cruises on a 40-nautical-mile grid pattern from San Francisco to Magdalena Bay have provided an immense (ca. 18,500 stations) data base for understanding the historical physical dynamics, chemistry, and biology of this region. The advent of the high-speed, large-capacity computer and the concurrent development of numerical analytic techniques may facilitate the manipulation and synthesis of large amounts of heavily intercorrelated data of this type.

This study applies factor analysis to the 1969 data, which include the first long-term sampling of chlorophyll, providing a trophic link between the physical-chemical milieu and the fish consumers.

METHODS

Complete data on 21 variables are available from 216 stations from 1969:

Northness (CalCOFI line number);

Temperature (°C), salinity (⁰/oo), and oxygen (ml/liter) at 10 m depth (Scripps Institution of Oceanography [SIO], unpublished data);

Nitrite, nitrate, phosphate, and silicate (mg-atoms/m³), chlorophyll and phæophytin (mg/m²; from data used in Thomas and Seibert 1974 and Owen 1974), integrated from the surface to 50 m;

Zooplankton volume (g/1000 m³), from surface to 150 m (NOAA/Southwest Fisheries Center [SFC], unpublished data);

Anchovy larvae (*Engraulis mordax*) in five size classes, integrated from the surface to 150 m: 1 = 2.0-3.0 mm, 2 = 3.5-5.0 mm, 3 = 5.5-8.0 mm, 4 = 8.5-12.0 mm, 5 = 12.5-ca. 25 mm (NOAA/SFC unpublished data);

Sardine larvae (*Sardinops caerulea*), 150 m to surface (NOAA/SFC unpublished data);

Hake larvae (*Merluccius productus*), 150 m to surface (loc. cit.);

Depth of the mixed layer (SIO unpublished data);

Distance offshore (nautical miles; SIO unpublished data);

Month of the year (SIO unpublished data).

Since oceanic ecosystems are complex and multidimensional and the available variables are numerous, factor analysis was used to reduce the number of variables to a minimum, without excessive loss of information, thus facilitating intelligible summarizations of the data.

Factor analysis is a statistical method that attempts to elicit normal multivariate structure of a universe in which many correlated variables can be sampled (Seal 1964). Factor analysis in research has been discussed at length by Cattell (1965 a, b) and by Rummel (1969) and Poole (1971), and its use in oceanographic work has been discussed by Kelly (1975), Angel and Fasham (1974), and Ebeling et al. (1970a, b).Stevenson et al. (1974) and Poole (1971) have examined the efficacy of combining environmental and species-abundance variables in common factor analysis. Colebrook (1974) has performed a principal-components analysis of major taxa groups in the California Current for the period 1955-59 in an attempt to explain their biomass fluctuations. Goodall (1954), Fisher (1968), Gittens (1968), and Echelle and Schnell (1976) have mapped factor scores and demonstrated the relationships between the generated factors and real environmental features.

The analytical method used was *R*-type factor analysis, wherein the matrix of product-moment coefficients is between variables rather than between units (see Kaiser 1958; Horst 1965). The program is available as part of the Statistical Package for the Social Sciences (SPSS: Nie et al. 1970) on the B-6700 computer at the University of California San Diego.

Station scores for each factor were computed, based on the annual pooled data, then mapped and contoured by hand.

The terms used in the Results and Summary and Conclusions that follow are here defined:

factor, a composite variable in which the relationship of the original variables is unique;

loading, the degree and direction of relationship of a variable to its factor, designated "alpha" (α);

communality, the amount of each variable's variation that is involved in the factors; the difference between communality and unity is the variable's "uniqueness," designated h^2;

correlation coefficient, here used to indicate residual relationship between factors before oblique rotation, designated r;

percent common variance, the amount of regularity accounted for by this factor in this data universe.

RESULTS

Analysis of 21 variables from 216 stations in the California Current in 1969 yielded seven factors (Figure 1):

Factor I, nutrient upwelling
Factor II, young anchovy and hake larvae;
Factor III, mixing;
Factor IV, thermal stratification;
Factor V, older anchovy larvae;
Factor VI, phytoplankton standing stock;
Factor VII, sardine larvae.

This is the minimum number of factors necessary to describe the relationships between the 21 variables without undue loss of information (they have eigen-values greater than 1.0, a criterion suggested by Nie et al 1970). The loadings (α) are the correlations of each variable to each factor. All variables participate in all factors to varying degrees, but those loadings less than .20 have been eliminated in order to simplify the table.

Pooled 1969 Data

Thirty-six percent of the common variance in the California Current in 1969 was due to nutrient upwelling regimes (Factor I), identified by low temperature, high salinity, and a shallow mixed layer, usually nearshore (see Yoshida and Mao 1957). The principal variables in this regime are the plant nutrient chemicals ($\alpha NO_3 = .94$; $\alpha PO_4 = .89$, $\alpha SiO_3 = .77$; $\alpha NO_2 = .53$). Zooplankton tends to be associated with this regime ($\alpha = .26$; see Figure 1).

Mixing regimes (Factor III) accounted for 18.0% of the regularity. These were identified by low temperature ($\alpha = -.68$), low salinity ($\alpha = -.98$), and high oxygen concentration ($\alpha = .60$). These regimes tended to be northerly and also had a positive zooplankton association ($\alpha = .34$).

Thermal stratification (Factor IV), which was identified by a very shallow mixed layer depth (α mixed layer depth $= -.69$), and warm surface water (α temperature $= .42$), accounted for 8.7% of the common variance.

Chlorophyll a and phæophytin as indices of phytoplankton standing stock (Factor VI) accounted for 6.3% of the common variance.

The larval fish seem to be related to two, and possibly three, different regimes:

1) Young anchovy and hake larvae (Factor II), accounting for 20.6% of the common variance, appear to be related to a separate set of conditions from

2) Older anchovy larvae (Factor V), which account for 7.3% of the variance in the data, and

3) Sardine larvae (Factor VII), which account for 3.0% of the variance in the data. Sardine larvae abundance is correlated to this factor ($\alpha = .43$) in which it is the principal loading.

The nutrient upwelling and mixing regimes are correlated at $r = .30$, whereas phytoplankton standing stock is correlated at $r = .45$ with nutrient upwelling and only at $r = .12$ with mixing.

Month-by-Month Analysis

The monthly trend maps are shown in Figures 2-7, their corresponding matrices as Appendix I-VI.

From January through May 1969, the communalities (h^2) were very low, suggesting that much of the variance could be accounted for by variables not measured, or that the variables tend to be more independent during those months, or that there were insufficient data per month to provide good convergence; the last appears more likely, since the annual pooled data showed good convergence (a rule of thumb for the design of a factor analysis is that the number of variables should not exceed the square root of the number of cases; John Senner, personal communication 1976). Nonetheless, some patterns are revealed by the analysis (Table 1).

January. In January primary and secondary production are low and related to phosphate and silicate concentration and a northern mixing regime. Nitrate concentration is related to upwelling more than to mixing. Nitrite concentration is related to zooplankton and older (8.5-25 mm) anchovy larval abundances. The younger (2-3 mm) anchovies appear to be independent of the older anchovies. Mixing processes account for 46.8% of the regularity in January, whereas upwelling is barely indicated in Factor VI, with 6.7% common variance.

Analysis of the January trend maps shows that mixing is occurring north of Point Conception and that there is some suggestion of a countercurrent south of there. Such a countercurrent has been previously demonstrated by Reid and Schwartzlose (1962) and others.

The stratification trend field is monotonous and negative (from -1.0 to -1.5), reflecting the fact that the current is unstratified at this time of year. The nutrient factor, which contains the upwelling component, is positive in coastal enclaves near San Francisco, off Monterey, south of Point Conception, and south of San Diego to Cape Colnett. The chlorophyll field is positive from San Francisco Bay to Monterey Bay and south of Point

UPWELLING PROCESS MIXING PROCESS

A. Oblique factor analysis of pooled 1969 CalCOFI data. Loadings less than 0.20 have been omitted for clarity.

NUTRIENTS — FACTORS — PRIMARY PRODUCTION

	1	2	3	4	5	6	7	Comm.	X̄	S
CalCOFI line								.80	98	--
Temperature	-.29		-.63	.42				.88	15.87	2.8
Salinity	.30		-.98					.88	33.51	.3
Oxygen			.60					.60	5.8	.4
Nitrite	.53						.29	.57	3.1	3.9
Nitrate	.94							.89	127.7	194.8
Phosphate	.89							.82	26.1	15.1
Silicate	.77							.67	280.4	270.8
Chlorophyll-a					1.00			.90	28.6	27.7
Phaeophytin					.59			.47	12.9	11.6
Zooplankton volume	.26		.34				.24	.31	191.8	311.3
Anchovy 2-3 mm		-.67						.48	1807.5	8672.2
Anchovy 3.5-5 mm		-.84						.65	1330.9	4762.3
Anchovy 5.5-8 mm		-.55			-.42			.65	701.6	1824.9
Anchovy 8.5-12 mm					-.89			.94	276.9	873.0
Anchovy 12.5-25 mm					.62			.42	49.4	186.6
Sardine larvae						.43		.23	3.7	21.2
Hake larvae		-.59						.42	314.9	1118.5
Mixed layer depth	-.24			-.69				.63	26.3	20.9
Distance offshore	-.40					-.20	-.20	.44	78.4	83.7
Month of year				.92				.91	--	--
% Common variance	36.1	20.6	18.0	8.7	7.3	6.3	3.0	# Cases = 216		

YOUNG ANCHOVY LARVAE

B. Correlation coefficients for factors on factors from analysis of pooled 1969 CalCOFI data.

OLDER ANCHOVY LARVAE

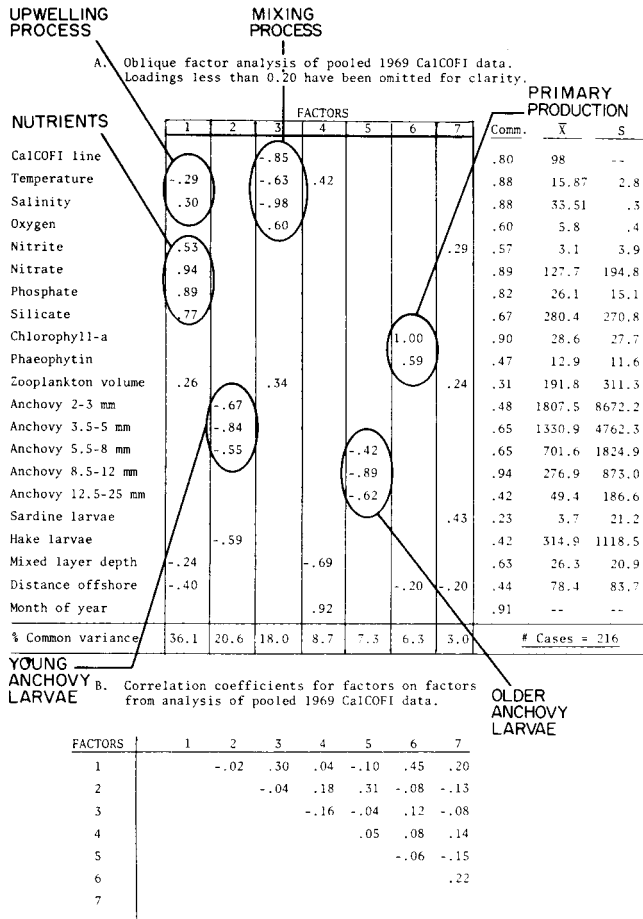| FACTORS	1	2	3	4	5	6	7
1		-.02	.30	.04	-.10	.45	.20
2			-.04	.18	.31	-.08	-.13
3				-.16	-.04	.12	-.08
4					.05	.08	.14
5						-.06	-.15
6							.22
7							

Figure 1. Descriptive interpretation of a factor analysis: the 1969 pooled data. Analyses for monthly data are given in the Appendix.

Conception. Young anchovy scores were highest in the Santa Barbara Channel. Older anchovy-larvae scores were highest from off Monterey south to Point San Martin, outside the Channel Islands, and in diminished strength from San Diego to Punta Eugenia.

February-March. In February mixing (20.9% common variance) is still responsible for primary production, but new nutrient input is provided by upwelling (37% common variance). The contours for the mixing factor are generally perpendicular to the coast, and the contour of the average mixing factor score has moved northward, suggesting that the net effect of mixing has been reduced. Northward movement of nearshore waters has disappeared. Both the stratification and nutrient (upwelling) factor contours are parallel the coast, and the positive zones are strongly concentrated into coastal pockets. The highest phytoplankton standing stock appears from Punta Descanso to Punta San Antonio, Baja California, included in a general high from Point Conception to Viscaino Bay. Younger and older anchovy larvae again are geographically separated.

TABLE 1

Percent Common Variance (Regularity) Accounted for by Each of Three Physical Regimes in the California Current for 1969.

	Jan.	Feb.	Apr.	May	Jul.	Sep.
Upwelling	6.7	37.0	38.7	39.8	37.2	(46.0)
Mixing	46.8	20.9	I	I	6.1	22.7
Stratification	(8.5)	(6.8)	12.9	7.3	44.2	8.8

Figures in parentheses indicate that identification is questionable due to low correlation of salinity and temperature to the factor. "I" indicates that the contribution of the regime is indeterminate with the technique used but that it is very low.

April. In April upwelling accounts for 38.7% of the common variance; the standing stock of phytoplankton (chlorophyll *a*) is strongly correlated to the upwelling factor ($\alpha = .37$), as are the principal plant nutrient chemicals (α NO$_3$ = .48; α PO$_4$ = .40; α SiO$_3$ = .36). The younger anchovy larvae occupy nearshore, more stratified waters, whereas distributions of older anchovy larvae seem more strongly influenced by zooplankton abundances.

May-June. In the May-June period, 39.8% of the regularity is accounted for by upwelling, which dominates the physical processes; the southern area is becoming more stratified, and some mixing is seen offshore in the north. The high-value nutrient trend lines hug the coast from San Francisco to Cape San Quintin. Chlorophyll *a* and fish larvae have an affinity for areas with shallow mixed layers. Mixing only accounts for 7.3% of the common variance. The zooplankton have a strong affinity for areas of high phytoplankton standing stock ($\alpha = .59$). The fish larvae picture is confused.

July. In July 44.2% of common variance is contained in a stratification factor, nearshore, which contains the principal primary production (α chl *a* = .84) and anchovy larvae components (α 2-3 mm = .96; α 3.5-5 mm = .67; α 5.5-8 mm = .86; α 8.5-12 mm = .94).

The fourth factor is negatively correlated to the stratification factor ($r = -.42$); if the signs of the loadings are reversed, the sign of the correlation coefficient may be reversed, and the sum of common variance accounted for by stratification processes is 50.3%.

Sardine and hake larvae were absent. Upwelled nutrients account for 32.7% of the common variance. Zooplankton abundance ($\alpha = .77$) and oldest anchovy larvae ($\alpha = .22$) are correlated with this regime. This factor is strongly nearshore (α offshoreness = -.59) and has a very shallow mixed-layer depth (α mixed-layer depth = -.61) component.

August-September. In September there is a general moderate nutrient abundance, strongest inshore and to the north of Point Conception. Zooplankton volume ($\alpha = .44$) and the two younger anchovy size classes ($\alpha = .50$ and .25 respectively) are correlated to this nutrient-containing factor. Standing stock of phytoplank-

Figure 2. Contour maps of station scores for each of seven factors in the California Current for January 1969.

Figure 3. Contour maps of station scores for each of seven factors in the California Current for February-March 1969.

Figure 4. Contour maps of station scores for each of seven factors in the California Current for April 1969.

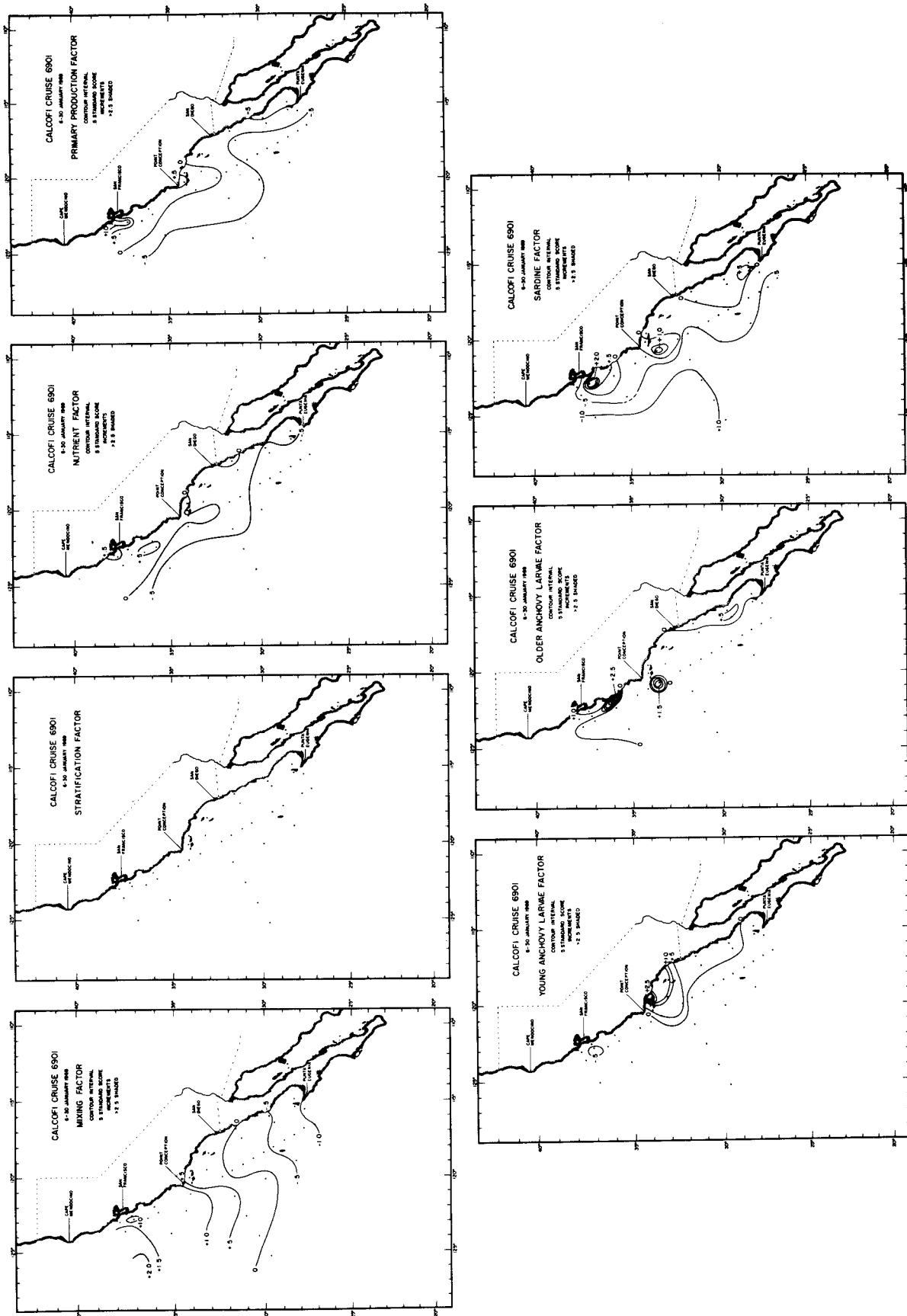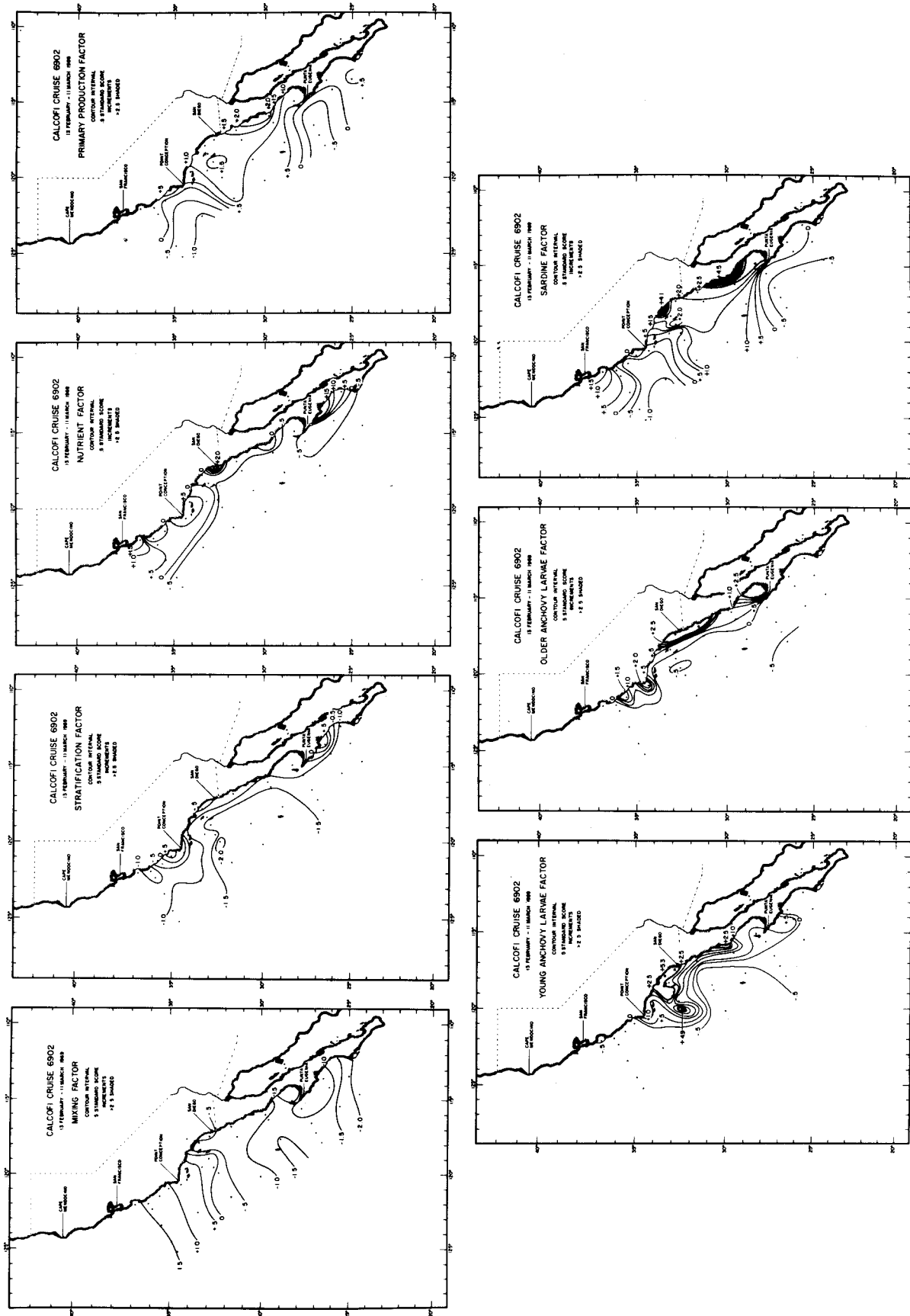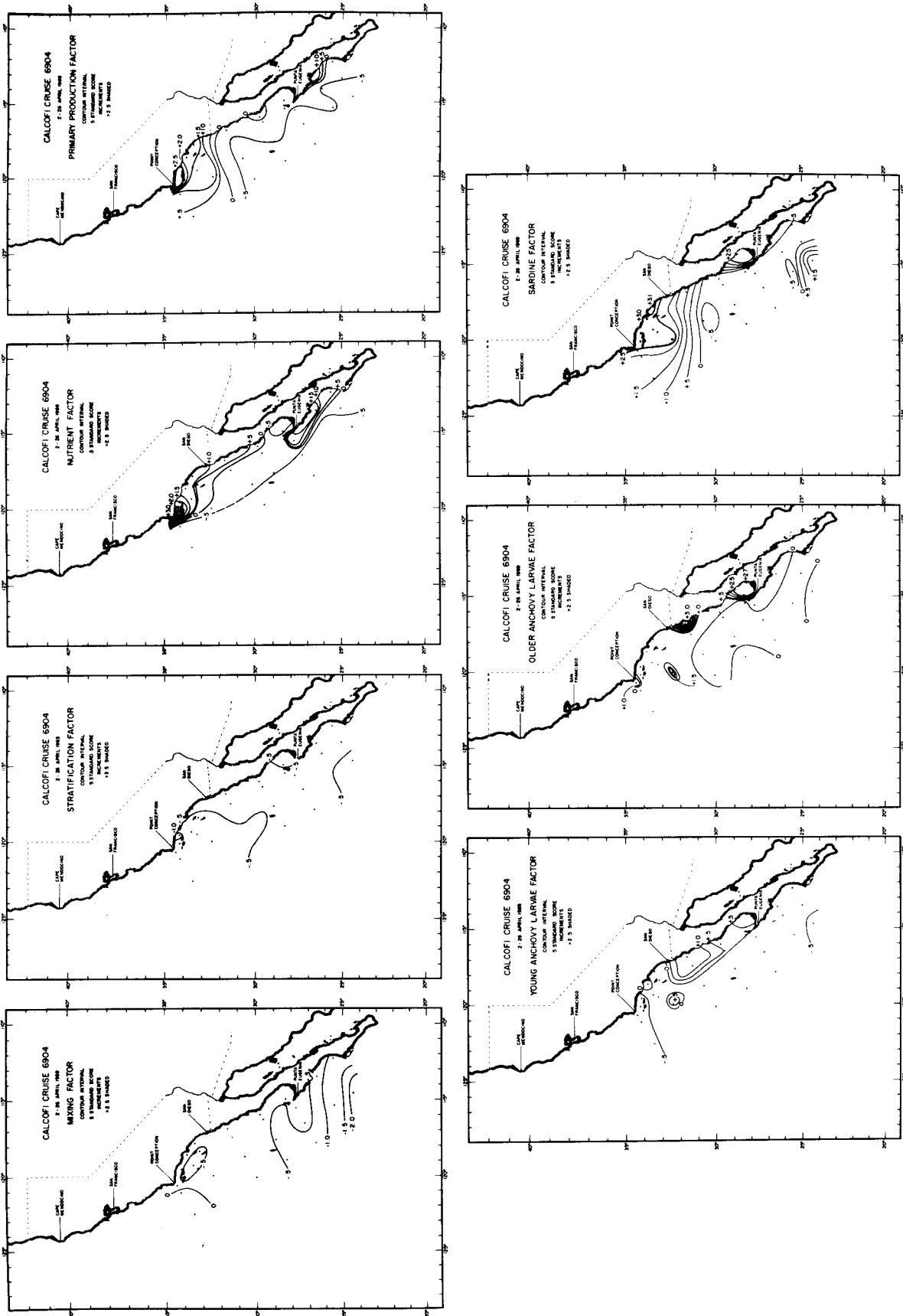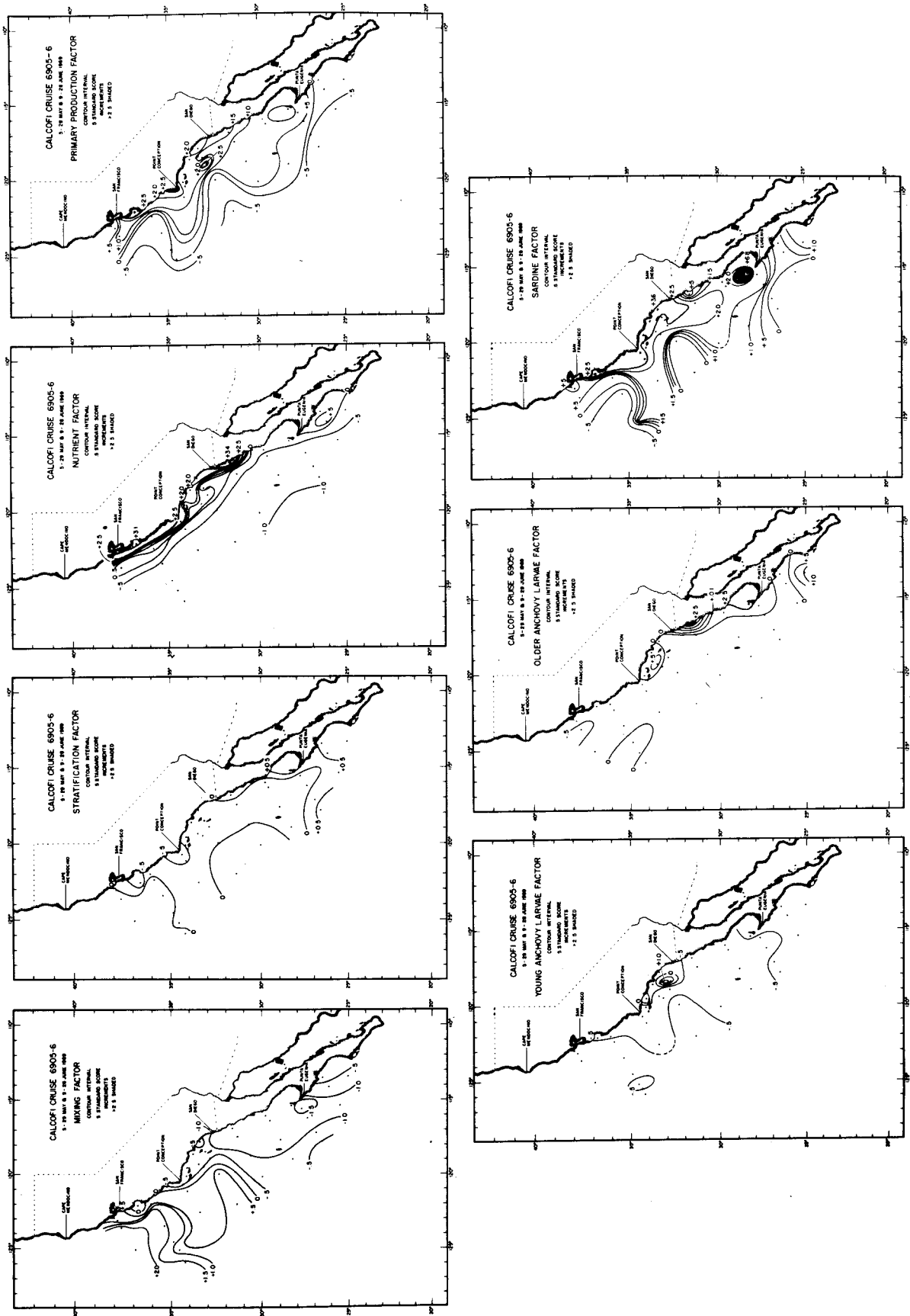Figure 5. Contour maps of station scores for each of seven factors in the California Current for May-June 1969.
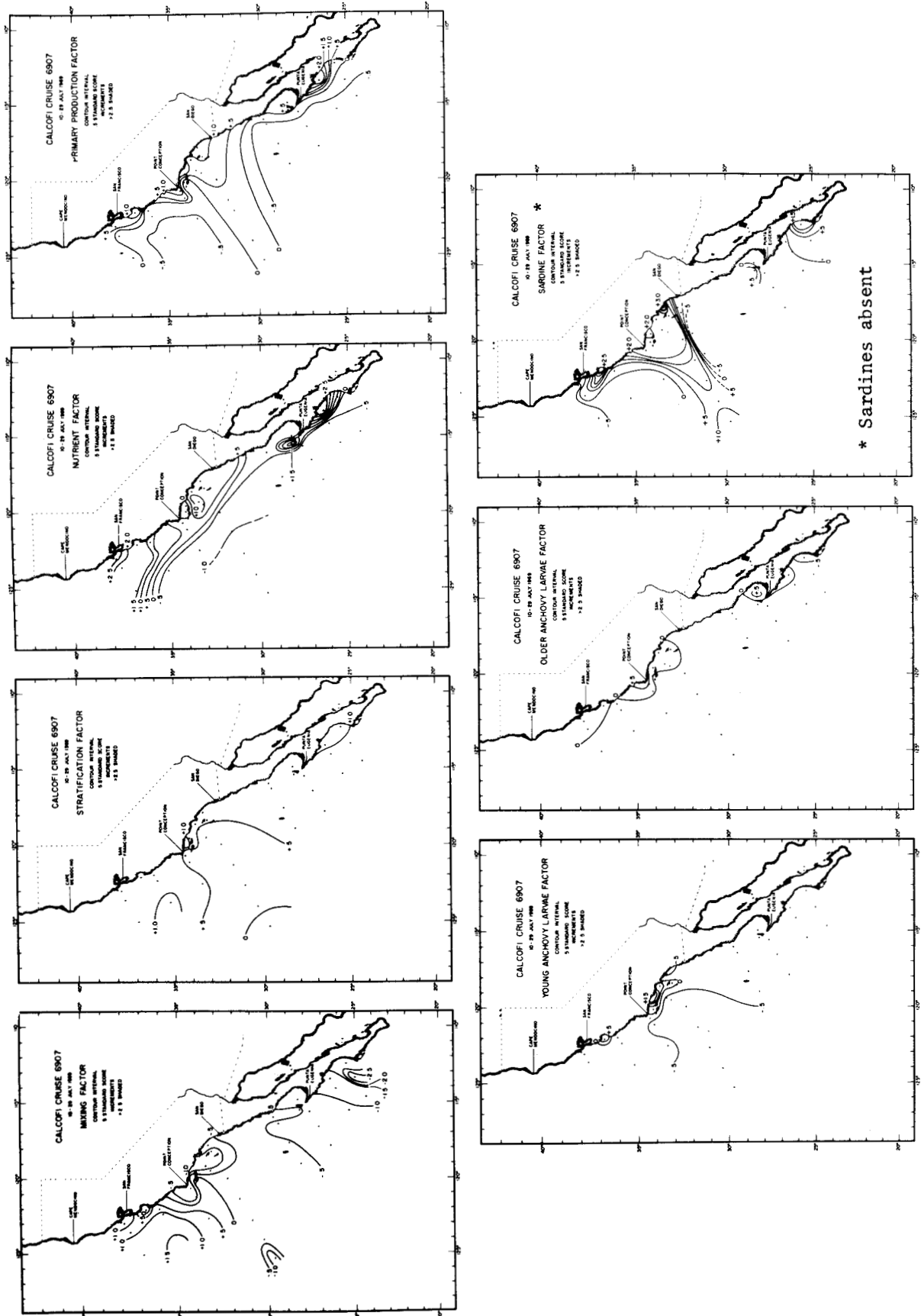
Figure 6. Contour maps of station scores for each of seven factors in the California Current for July 1969.
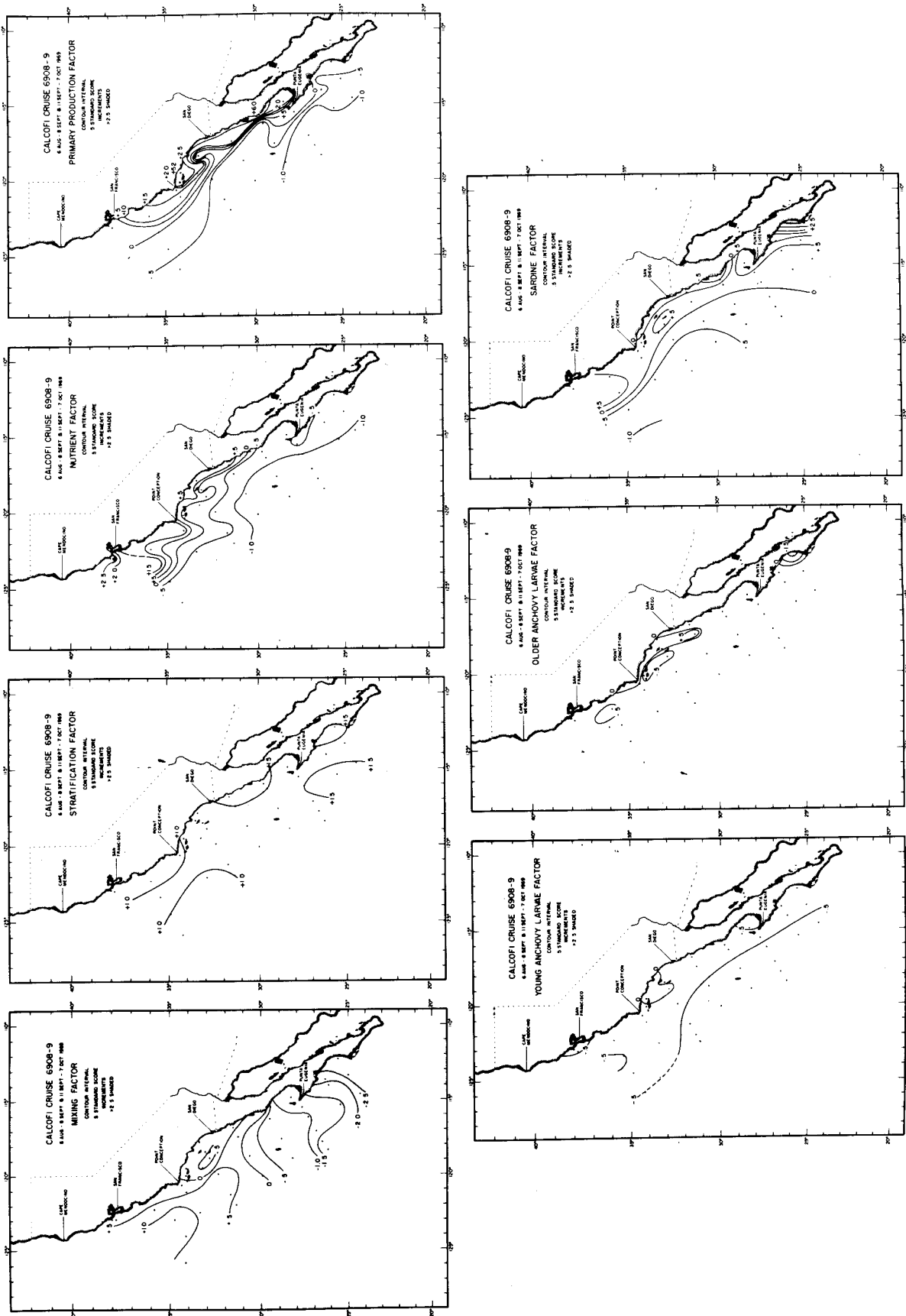
Figure 7. Contour maps of station scores for each of seven factors in the California Current for August-September 1969.

ton (α chl $a = -.22$) is negatively correlated with this factor but is positively correlated to two other factors: a mixing factor ($\alpha = .20$) and a nearshore, shallow mixed-layer factor ($\alpha = .56$). The nutrient factor, the mixing factor, and the shallow-mixed-layer factor account for 46%, 22.7%, and 8.8%, respectively, of the common variance.

DISCUSSION

Physical Relationships

The three major physical regimes identified in this work were upwelling, mixing (advective + local), and stratification. These accounted for 36%, 18%, and 8.7% respectively, of the common variance in the year's pooled data. The contribution of each on a seasonal basis to the common variance (regularity) in this data universe is shown in Table 1, which suggests that mixing processes dominate the early months, that upwelling processes dominate from February through about May, that stratification processes dominate in midsummer, and that upwelling is again dominant in September. Mixing and stratification tend to be uncorrelated or inversely correlated.

A comparison of a chart of dynamic height anomalies for January of 1969 (Scripps Institution of Oceanography 1976) with a Primary Production Factor Score chart will suggest that higher production levels occur where the nearshore contours of dynamic height anomaly run south-to-north and that negative scores nearshore occur where the contours run north-to-south. This is in accord with the findings of Yoshida and Mao (1957) that the subsurface, poleward component of the nearshore current is associated with ascending motion, i.e. upwelling. Nutrient-factor score maps for 1969 suggest that there is a tendency toward coastal upwelling all year but that greater intensities occur in later spring and early summer. Bakun (1973, p. 10, Figure 6) demonstrates that there is always a positive upwelling index along the coast of the Californias and that this intensity peaks during May, June, and July.

Chemical-Primary Production Relationships

Taken for 1969 as a whole, the four nutrient chemicals studied are correlated to a factor that is related to upwelling processes, but each of the separate cruises has a somewhat different distribution of relationships. In January phosphate and silicate contribute to the mixing factor, whereas nitrate is negatively correlated and nitrite is uncorrelated. Both nitrite and nitrate are positively is uncorrelated. Both nitrite and nitrate are positively correlated to an upwelling factor. Nitrite is also positively correlated to zooplankton and older anchovy larval abundance. This suggests that the mixed water is nitrogen-

depleted and perhaps that primary production in such water is nitrogen-limited. The nearshore water, where upwelling is occurring, is not nitrogen-depleted, and the highest standing stock of phytoplankton is in these coastal pockets. The correlation of nitrite to abundances of secondary producers suggests that this nitrogen is a metabolic byproduct or excretory product.

In February, all four nutrients contribute to the upwelling factor. Nitrite remains, however, also correlated to abundances of fish larvae. The only significant phytoplankton standing stock is also correlated to this factor.

The correlation of nitrite and nitrate concentration to phytoplankton standing stock suggests that primary production at this time of year in the California Current system is nitrogen-regulated and that the species comprising this stock may be especially adapted to use excreted nitrite precursors or nitrite (cf. Grenney et al. 1973; Caperon and Meter 1972a, b; Newell et al. 1972; Strickland et al. 1969), as well as nitrate. *Biddulphia aurita*, a cosmopolitan centric diatom, when cultured with nitrate-nitrogen, excreted nitrite-nitrogen, which it was then able to utilize (Liu and Roels 1972).

One may view this winter production as a nitrogen feed-back system, whose effect is extended both temporally and spatially by zooplankton and phytoplankton excretion of nitrite precursors.

By April the effect of upwelling on primary production is great; chlorophyll a distribution and concentration are correlated to upwelled water containing the three more conservative nutrients. Nitrite remains uncorrelated to the other nutrients but is highly correlated to the factor containing strong loadings for phæophytin, a photosynthetically inactive degradation product of chlorophyll, and for zooplankton abundance. This tends to reinforce the thought that nitrite, as perceived at the resolving power of this numerical analysis, and when not correlated to the other nutrients, is an excretion product.

In May chlorophyll a, phæophytin, and zooplankton are strongly intercorrelated, probably in this way: chlorophyll a represents standing stock of the first trophic level; the zooplankton, the grazers; and phæophytin, the product and evidence of zooplankton feeding (in fecal pellets, particles of dead cells; Lorenzen 1965). That primary production is in another factor, separate from that containing the nutrients, suggests that chlorophyll a, phæophytin, and zooplankton have more intercorrelation and interdependence for abundance and distribution than they have with the nutrients. There is a hint of correlation between the two factors, but so much variance in this small number of cases (22) has been accounted for within factors that there is little resolution to the matrix of correlation between factors. This is a problem throughout the month-by-month analyses.

Sufficient of the nitrite in the system is now accounted

173

for by direct upwelling that a portion of it is correlated to the factor containing the other nutrients, but a portion of it remains correlated to a factor containing heavy loadings for some fish and may be assumed to be an excretion product.

In July stratification, upwelling, and mixing processes account for 44.2%, 37.2%, and 6.1%, respectively, of the common variance. Stratification and mixing are negatively correlated ($r = -.42$). The phytoplankton standing stock is strongly correlated to the stratification factor ($\alpha = .84$) and uncorrelated to either upwelling or mixing. Since the season of maximum upwelling has just ended, the coastal waters could be considered to be generally enriched. Zooplankton abundance is high, so their excretion products are abundant. I suggest that in summer, coastal waters continue to be enriched by moderate upwelling, which provides a cooler habitat for zooplankton ($\alpha = .77$ on upwelling), whereas the really tremendous numbers and concentrations of phytoplankters occur in stratified, recently enriched waters. The fact that the trend maps of the pooled annual data factor scores for stratification and for the nutrient factor (which contains the upwelling component) overlap positively suggest that there is little gross geographic separation of these two influences at this time of year; in other words, that upwelled water quickly becomes stratified and that the upwelling is concentrated in small localized plumes and domes.

By September, the coastal waters have become generally destratified (stratification = 8.8% common variance), and mixing processes have become much more dominant (22.7% common variance). Nonetheless, phytoplankton standing stock remains highly correlated to stratification ($\alpha = .56$), although slightly correlated to mixing ($\alpha = .20$) and negatively correlated to upwelling ($\alpha = -.22$). New nutrient input (PO_4, SiO_3, NO_3) remains correlated to upwelling processes. Although there is evidence of change toward the winter mixing regime, the base of primary production seems to remain that of the midsummer; i.e. dependent on recently enriched but stratified water.

The Fish Larvae

Anchovies

Analysis of the annual pooled data factors reveals that distributions of the younger anchovy larvae are related to different parameters than are those of older fish and that this separation occurs somewhere between 5.5 and 8 mm length.

Lasker et al. (1970) have shown that first-feeding anchovy larvae (to age 8 days = ca. 5 mm; see Kramer and Zweifel 1970) can survive on a diet of the dinoflagellate, *Gymnodinium splendens*, but their growth on this diet falls off rapidly after ten days (Hunter 1976). During this same period they are intermittent swimmers (Hunter 1972) and require high densities of particles, upward of 40 *Gymnodinium*/ml, in order to ensure successful feeding and survival (Lasker 1975). To aid in this, yolk sac larvae (prior to first-feeding) are actively attracted to *Gymnodinium* swarms (Hunter and Thomas 1973).

Anchovy larvae begin to take small copepod nauplii at about 5 mm (Theilacker, personal communication 1977), but their success rate is below 40% at this stage (Hunter 1972). In Lasker's et al. (1970) experiments, larvae were capable of taking *Artemia salina* (brine shrimp) nauplii at about 8 mm (20 days).

One must assume that these larvae change their feeding tactics at about this age in order to obtain sufficient energy. If they were to continue taking dinoflagellates, they might be assured of successful feeding strikes, but insufficient nutrition, as they grow larger; however, the change to a diet of nauplii would likely involved wider ranging search patterns for a much less concentrated prey. Large concentrations of dinoflagellates must depend on rather calm, stratified, or very slowly upwelling water. Hence, one would not expect to find significant numbers of first-feeders surviving in wind-whipped or rapidly upwelling waters. The older larval stages, however, would not be expected to be so dependent on calm conditions.

Therefore, one may postulate a real difference in habitat requirements occurring at about the 5.5-8 mm size class as predicted by this analysis.

Given that larvae in general have a unique existence and need to survive, as well as a double task to accomplish—both to distribute the species and to grow up to become reproductive adults (Garstang 1928)—we can predict not only this change in habitat but also a series of changes in habitat requirement during the course of maturation. These may be rather drastic, as in the present situation, or gradual; the more gradual the change in requirements, the less amenable to numerical analysis will they become. Kramer and Zweifel (1970) have shown that the food requirements change gradually up to metamorphosis. So it appears that the most drastic, and therefore most likely to be confounded, change in habitat requirement is that from yolk sac to independence from the stratified conditions.

It appears that the sustaining nurseries for the northern anchovy are the Catalina Eddy and Viscaino Bay. In the spring of the year, the belt of water from San Francisco Bay to Point Conception is a large contributor, and at various times of the year the waters from Punta Engenia to Cabo San Lucas are a refuge (Kramer and Ahlstrom 1968). Both the Catalina Eddy and Viscaino Bay can be considered semi-closed gyral systems (Wyllie 1961; Schwartzlose 1962; Reid et al. 1958; Groves and Reid 1958; Fleming 1939). These eddies and the longshore

currents that connect them may serve to keep the majority of the young larvae from being swept out of their habitat and lost through dispersal. Kramer and Ahlstrom (1968) show a presence of anchovy larvae in these two eddies throughout the year, even when more offshore waters are essentially devoid of larvae. This fact is also demonstrated in the two anchovy larvae factor score maps for each month of 1969 in this study. Although the factor analytical tables are inconclusive, the factor score maps also show that areal distributions of higher factor scores for Factors II and V (young anchovy and hake larvae and older anchovy larvae) are coincident with higher scores for nutrient upwelling and stratification throughout the year.

Sardines

Higher sardine larvae factor scores throughout the year are also associated with the two eddies and the long-shore currents that connect them. Sardines were absent during July, so the sardine factor chart for July primarily reflects the abundance of nitrite, the second highest correlate to that factor.

Although the low correlation to any factor might suggest depression due to species interaction (i.e. anchovy versus sardine), the low communality suggests that the sardine larvae were simply not sampled in sufficient numbers to indicate their relationship to other variables. The implications of this are important in future sampling tactics, as well as in the use of existing data, for understanding larval sardine ecology.

The total lack of sardine larvae in the July collection is not surprising since population levels were depressed and larval abundances are typically low in the summer (Kramer 1970).

Hake Larvae

Hake larvae data also suffered from persistently low communalities and frequent zero capture rates, although they seemed to bear some general positive relationship to the distributions and abundances of some classes of anchovy larvae. The absence of hake larave in July and September and the lower abundance in May have been documented previously by MacGregor (1971). The persistent relationship with young anchovies may be due to a need for a common prey or to predation by hake larvae on anchovy larvae (DeWitt 1952).

Other Biological Relationships

Colebrook (1974) performed a principal components analysis on 17 taxonomic assemblages, without reference to environmental variables. There is little doubt that the pattern of distribution in Colebrook's first component is very similar to that of Factor III (mixing) and that that of his second component is strikingly similar to that of Factor I (nutrient-upwelling). This set of results suggests that there are at least two principal axes to zoogeographic distributions and abundances in the California Current area: the upstream-downstream (north-south, cold-warm, rich-depleted) axis and the onshore-offshore (shallow-deep, coastal-oceanic, rich-depleted) axis.

A third physical factor (thermal stratitifaction, Factor IV) may be a partial inverse of Factor III (mixing; $r = -.16$). This stratification factor has a distribution pattern similar to that of some species of zooplankters found in the California Current (see various CalCOFI Atlases), as do mixing and nutrient-upwelling. Zome zooplankton distributions suggest that a fourth physical factor, the partial inverse of nutrient upwelling (Factor I), may exist. That hypothetical factor should represent the influence of the Central Pacific Water mass and may appear in future work involving a large data universe. Some zooplankters having distributions similar to that of Factor I are larval Engraulis mordax (northern anchovy), larval Sardinops caerulea (Pacific sardine), and the copepod Calanus pacificus (shared with Factor III). The larvae of the hake, Merluccius productus, have an inverse distribution to the factor, since they are spawned off Baja California and are carried northward (Alverson and Larkins 1969; Nelson and Larkins 1970). Limacina helicina (Mollusca; Thecosomata), Calanus cristatus, C. plumchrus, and Candacia columbiae (all Copepoda) are examples of some zooplankters having distributions similar to Factor III. Calanus robustior, C. gracilis, C. minor, and Limacina inflata are examples of some zooplankters with distributions similar to Factor IV (see Fleminger (1964) and McGowan (1967) for distributions of copepods and molluscs, respectively).

SUMMARY AND CONCLUSIONS

The use of factor-analysis and factor-score mapping has revealed identifiable characteristics of the California Current. These characteristics are understandable within the context of classical concepts of physical, chemical, and biological dynamics and distributions.

Three physical regimes have been described numerically: mixing processes (low temperature, low salinity, high oxygen); upwelling processes (low temperature, high salinity); and thermal stratification processes (high temperature, high salinity, shallow mixed layer). Phytoplankton nutrient chemicals (PO_4, NO_3, SiO_3) tend to co-occur with mixing and upwelling processes. Nitrite tends to be associated with thermally stratified waters during the summer. High chlorophyll abundances are associated with mixing and upwelling regimes, but first-feeding and very young anchovy larvae are associated with upwelled and stratified waters. The 2-to-5 mm and the 8-to-25-mm size classes of anchovy larvae tend to have mutually exclusive distributions.

The annual cycle for 1969 began in winter with domination by mixing processes, was later (March-June) dominated up upwelling processes, became stratified in late summer, and began mixing again in the autumn.

Factor analysis is amenable to the study of other interrelationships between a much larger number of biological variables. To diminish the number of redundant variables, composite variables of the chemical and physical features of the environment could be formed. These process or concept variables, such as mixing index, upwelling index, stratification index, plant-nutrient index, and productivity index, could be entered with the biological variables. Better definition of the ecosystem may result as other untapped sources of historic data become available.

Analysis of the latent roots of the factor matrices may provide predictive capacity for fishery stock management once basic relationships between age classes of species and ambiental variables have been better defined numerically.

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APPENDIX
I – January

A. Oblique factor analysis of January 1969 CalCOFI Data. Loadings less than 0.20 have been omitted for clarity.

	1	2	3	4	5	6	7	Comm.	X̄	S
CalCOFI line	−.37							.15	91	−
Temperature	−.35							.14	14.74	1.76
Salinity	−.33							.14	33.44	.29
Oxygen				−.57				.36	5.91	.20
Nitrite			−.30			.26		.20	3.27	3.07
Nitrate	−.26					.21		.16	56.08	69.34
Phosphate	.25							.12	20.54	7.93
Silicate	.35							.16	270.45	266.80
Chlorophyll-a	.39							.18	21.57	10.31
Phaeophytin	.33							.15	12.26	6.90
Zooplankton volume	.20		−.25					.16	97.29	78.41
Anchovy 2-3 mm		.23			.83			.72	1574.23	7230.64
Anchovy 3.5-5 mm		−.34			.48			.36	1389.97	4246.30
Anchovy 5.5-8 mm		−.59						.34	529.50	1559.30
Anchovy 8.5-12 mm			−.63					.40	225.29	718.46
Anchovy 12.5-25 mm			−.64					.42	34.47	186.76
Sardine larvae				−.77				.60	.84	5.19
Hake larvae		−.62						.38	164.50	436.75
Mixed layer depth						−.67		.49	43.7	12.18
Distance offshore						−.58		.37	95.2	−
Month of year										
% Common Variance	46.8	17.8	13.0	8.5	7.1	6.7		# Cases = 38		

B. Correlation coefficients for factors on factors, factor analysis of January 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		.03	−.04	−.03	−.02	.06	
2			−.02	−.05	−.06	.05	
3				.01	.04	−.11	
4					−.04	.06	
5						−.11	
6							
7							

II – February

A. Oblique factor analysis of February 1969 CalCOFI data. Loadings less than 0.20 have been omitted for clarity.

			FACTORS								
	1	2	3	4	5	6	7	Comm.	$\overline{X}$	S
CalCOFI line			−.47					.22	99	–
Temperature			−.41					.19	14.52	1.79
Salinity			−.45					.21	33.52	.35
Oxygen			.39	.44				.36	5.90	.32
Nitrite	.33			.22				.21	3.22	3.27
Nitrate	.47							.22	79.92	113.13
Phosphate	.47							.22	22.82	9.07
Silicate	.47							.22	188.95	131.82
Chlorophyll-a			−.26	.25				.17	26.82	11.06
Phaeophytin			−.35					.17	10.84	6.71
Zooplankton volume	.28							.11	200.82	534.34
Anchovy 2-3 mm					−.49			.27	5900.21	17985.6
Anchovy 3.5-5 mm					−.69			.49	4146.47	9683.03
Anchovy 5.5-8 mm		.42			−.24			.24	1679.55	2989.32
Anchovy 8.5-12 mm		.53						.29	570.68	1073.85
Anchovy 12.5-25 mm		.54						.33	119.11	304.82
Sardine larvae				.66				.44	2.66	12.13
Hake larvae				.44	−.32			.32	1259.97	2271.98
Mixed layer depth	−.20							.12	48.16	2.30
Distance offshore	−.22	−.34						.19	68.68	–
Month of year										
% Common Variance	37.0	23.8	20.9	11.4	6.8			# Cases = 38		

B. Correlation coefficients for factors on factors, February 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		.02	.03	.06	.02		
2			−.03	.07	−.01		
3				−.04	.02		
4					−.00		
5							
6							
7							

III – April

A. Oblique factor analysis of April 1969 CalCOFI data. Loadings less than 0.20 have been omitted for clarity.

	FACTORS 1	2	3	4	5	6	7	Comm.	X̄	S
CalCOFI line				.54				.30	106	–
Temperature	−.22			.34				.20	14.96	1.71
Salinity				.54				.33	33.57	.23
Oxygen	−.29				.71			.56	5.68	.29
Nitrite					.53			.32	2.87	5.47
Nitrate	.48							.24	184.21	233.76
Phosphate	.40							.22	31.55	18.16
Silicate	.36							.16	345.17	294.98
Chlorophyll-a	.37							.16	26.54	18.39
Phaeophytin				−.24	.25			.17	11.41	8.81
Zooplankton volume		−.27			.23			.18	149.79	151.60
Anchovy 2-3 mm			−.62			−.30		.47	1316.48	2896.49
Anchovy 3.5-5 mm			−.56					.36	811.03	1331.57
Anchovy 5.5-8 mm		−.32				.42		.33	1020.79	2194.70
Anchovy 8.5-12.5 mm		−.64						.42	539.17	1437.44
Anchovy 12.5-25 mm		−.56						.33	64.59	138.90
Sardine larvae						.81		.67	1.07	5.76
Hake larvae				−.31				.15	466.17	938.81
Mixed layer depth			.41					.24	2.66	1.17
Distance offshore	−.27		.29					.19	5.72	
Month of year										
% Common Variance	38.7	17.8	13.5	12.9	10.4	6.7			# Cases = 29	

B. Correlation coefficients for factors on factors, April 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		−.04	−.03	.03	.09	−.01	
2			.03	.08	−.02	−.06	
3				−.06	−.03	−.06	
4					−.01	.00	
5						−.06	
6							
7							

IV – May

A. Oblique factor analysis of May CalCOFI data. Loadings less than 0.20 have been omitted. 12.5-25 mm anchovies were completely absent, and omitted from the matrix.

| | FACTORS | | | | | | | | | |
	1	2	3	4	5	6	7	Comm.	$\overline{X}$	S
CalCOFI line					.54			.33	77	–
Temperature	−.20	−.29			.24			.21	13.46	1.35
Salinity	.44			−.21	.25			.33	33.28	.35
Oxygen			.41	.30	−.44			.45	6.31	.27
Nitrite	.26			.20				.15	5.56	5.00
Nitrate	.44							.19	273.86	275.10
Phosphate	.42							.19	34.74	19.11
Silicate	.44							.20	389.91	286.01
Chlorophyll-a						−.54		.33	35.80	29.32
Phaeophytin						−.50		.29	25.88	18.20
Zooplankton volume	−.22				−.27	−.59		.47	420.14	406.08
Anchovy 2-3 mm		−.55	−.23	.25				.43	510.95	1378.26
Anchovy 3.5-5 mm			.60					.39	509.86	1222.69
Anchovy 5.5-8 mm			.57					.35	623.05	1780.25
Anchovy 8.5-12 mm		−.55			−.25			.38	49.68	132.79
Sardine larvae				.77				.60	3.95	18.54
Hake larvae		−.47						.27	13.68	26.75
Mixed layer depth				−.31	−.39	.20		.30	9.5	8.4
Distance offshore	−.24							.13	70.0	–
Month of year										
% Common Variance	39.8	22.5	14.1	10.4	7.3	5.9			# Cases = 22	

B. Correlation coefficients for factors on factors, May 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		−.02	.01	.04	−.05	−.08	
2			−.04	.01	.01	.03	
3				−.09	.01	−.00	
4					−.04	−.07	
5						.01	
6							
7							

V – July

A. Oblique factor analysis of July 1969 CalCOFI data. Sardine and hake larvae have been omitted from the matrix since they were compeletely absent. Loadings less than 0.20 have been omitted for clarity.

	FACTORS							Comm.	$\bar{X}$	S
	1	2	3	4	5	6	7			
CalCOFI line		−.53		−.65				.72	80	–
Temperature	.26	−.66		−.50				.83	16.05	2.18
Salinity	.30	.64		−.41				.80	33.42	.27
Oxygen	.24		−.67					.55	5.81	.47
Nitrite		.81						.68	3.95	4.27
Nitrate		.76	−.30					.71	162.00	204.18
Phosphate		.80						.65	34.94	12.05
Silicate		.96	.29					.97	338.13	342.99
Chlorophyll-a	.84		−.21					.85	53.82	53.11
Phaeophytin	.44	.24	.20	−.48				.70	23.45	21.93
Zooplankton volume		.77						.63	253.00	201.49
Anchovy 2-3 mm	.96		.28					.90	189	494
Anchovy 3.5- mm	.67		.38	−.34				.85	451	1005
Anchovy 5.5-8 mm	.86							.90	268	440
Anchovy 8.5-12 mm	.94		−.28					.88	102	195
Anchovy 12.5-25 mm		.22	−.67	−.20				.53	12	28
Mixed layer depth	−.22	−.61	.23	.24				.62	16.2	13.1
Distance offshore	−.38	−.59	.26	.23				.75	83.7	–
Month of year										
% Common Variance	44.2	37.2	12.5	6.1					# Cases = 16	

B. Correlation coefficients for factors on factors, July 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		.06	−.09	−.42			
2			−.06	−.01			
3				−.00			
4							
5							
6							
7							

VI – September

A. Oblique factor analysis of September 1969 CalCOFI data. Loadings less than 0.20 have been omitted for clarity. Hake larvae were completely absent and have been omitted from the matrix.

	1	2	3	4	5	6	7	Comm.	$\overline{X}$	S
			FACTORS							
CalCOFI lines		−.43						.20	118	–
Temperature		−.45						.22	20.99	2.51
Salinity		−.47						.23	33.75	.33
Oxygen		.40						.21	5.29	.38
Nitrite		−.22			−.72			.58	2.18	3.46
Nitrate	.46							.22	16.45	51.97
Phosphate	.37							.15	12.31	7.25
Silicate	.23				−.36			.20	122.00	116.92
Chlorophyll-a	−.22	.20		.56				.40	37.37	54.40
Phaeophytin				.44				.23	10.02	5.67
Zooplankton volume	.44							.20	58.80	36.76
Anchovy 2-3 mm	.50							.25	22	69
Anchovy 3.5-5 mm	.25	−.25						.16	8	19
Anchovy 5.5-8 mm			−.54					.30	29	89
Anchovy 8.5-12.5 mm			−.57					.33	46	205
Anchovy 12.5-25 mm			−.57					.33	10	43
Sardine larvae				.26	.44			.31	11	49
Mixed layer depth				−.37	−.29			.27	16.5	12.7
Distance offshore				−.42				.23	86.5	–
Month of year										
% Common Variance	46.0	22.7	15.5	8.8	6.9				# Cases = 20	

B. Correlation coefficients for factors on factors, September 1969 CalCOFI data.

FACTORS	1	2	3	4	5	6	7
1		−.01	−.03	.06	−.00		
2			.01	−.03	−.05		
3				−.04	−.03		
4					.03		
5							
6							
7							

THALIACEA OF THE CALIFORNIA CURRENT REGION: RELATIONS TO TEMPERATURE, CHLOROPHYLL, CURRENTS, AND UPWELLING

MAURICE BLACKBURN
Institute of Marine Resources[1]
University of California San Diego
La Jolla, California 92093

ABSTRACT

Thaliacea are a major component of herbivorous zooplankton biomass in the upper layers of warm seas and are able to colonize areas where conditions are suitable at a faster rate than other herbivores. An attempt was made to relate distribution and abundance of the principal species of the California Current region to distributions of their food (measured as chlorophyll a), temperature, surface currents, and indices of upwelling. Data of all cruises made in the region in 1969, when all the required kinds of data were available, were used.

The three most abundant species of Thaliacea were *Dolioletta gegenbauri*, *Doliolum denticulatum*, and *Thalia democratica*. *Dolioletta* is a cool-water form whose southern limit of range approximates the 15°C isotherm at 10 m. It lives in the California Current and is always present close to shore in waters of suitable temperature. Thus, it can become abundant in areas where chlorophyll is most plentiful, and most observations are consistent with such a population increase. The range of *Doliolum* is limited by temperature in a different way, the northern range limit being about the position of the 13°C isotherm at 10 m. It enters the region from the west and becomes abundant when it reaches phytoplankton-rich coastal waters of suitable temperature. *Thalia* occurs in slightly warmer water than does *Doliolum*. It enters the region from offshore but does not reach the coast during most of the year and never attains maximum abundance there. It is most abundant in offshore waters of low chlorophyll, unlike *Dolioletta* and *Doliolum*.

The question was posed as to why Thaliacea do not dominate the zooplankton of coastal upwelling areas. In the region studied, the offshore Ekman transport prevents *Dolioletta* from becoming dominant close inshore in the early part of the upwelling season, although it can become dominant there later. *Doliolum* is sometimes prevented from reaching the coast by the velocity of the California Current, and when it does arrive it is sometimes excluded from the most inshore rich waters by low temperature. *Thalia* seldom reaches the coast, for reasons which are not clear.

INTRODUCTION

Thaliacea (salps, doliolids, and pyrosomes) are filter-feeding holoplankters, whose diet is mostly phytoplankton. They are frequently a major component of zooplankton biomass in the upper waters of warm and temperate seas (e.g. Thompson, 1948; Tranter 1962; Furnestin 1970; De Decker 1973). Their ecology is less known than that of other major herbivore groups, but several interesting studies have been made recently on salps. Silver (1971) and Heron (1972a, b) demonstrated remarkably high rates of growth of individuals and population in *Salpa fusiformis* and *Thalia democratica*, respectively. Heron found that growth in length was over 10%/hour during much of the life cycle in both the solitary and aggregate forms. The complete cycle of two generations was completed in two days to two weeks, being longer when food was scarce or temperature low. In the 2-day case the population was increasing in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal.

Silver and Heron characterized salps as opportunists or colonizers, better able than other herbivores to respond to phytoplankton blooms by rapid population growth. Salps often appear in very dense swarms. some of which have been correlated positively with phytoplankton and negatively with crustacean herbivores (Berner 1957; Fraser 1961; Humphrey 1963; Sheard 1965). The ability of salps to increase greatly probably reflects their high efficiency in obtaining food. Rates of filtration can exceed 100 ml/minute in large individuals (Harbison and Gilmer 1976). Food particles from 1 μm to 1 mm are taken unselectively (Madin 1974). On the other hand, salps seem to have few abundant predators, although the list of those known is growing (Silver 1971, 1975; Heron 1973; Hamner et al. 1975).

Assuming that these features of ecology apply to some extent to other Thaliacea as well as salps, it appeared that a study of thaliacean distribution in relation to temperature, phytoplankton, and currents would be of interest. Temperature, food, and currents are generally considered the major determinants of distribution of epipelagic animals both areally and temporally, but I have sometimes experienced difficulties in relating various kinds of animals to them. The animal of interest may have a varied diet, increasing the difficulty of defining the distribution of its food. If it is planktonic, its own distribution can be described from net catches made on a research ship, but relations to the distribution of its food may be obscured by its drift in currents. If the animal is nektonic, it can search for food and aggregate upon it independently of water movements if temperatures are suitable, but its own distribution may be hard to define unless fishing can be done. With Thali-

[1]Present address: 741 Washington Way, Friday Harbor, Washington 98250.

184

acea it seemed for reasons given above that food distributions could be defined approximately from measurements of chlorophyll *a* and that the animals should remain abundant in the presence of plentiful food (and suitable temperature) even though subject to drift. High abundance of Thaliacea in an area of high phytoplankton concentration would not necessarily signify the drifting in of a swarm but more probably its generation in situ from a diffused "seed" population.

It was hoped that the proposed study would answer a special question; namely, why Thaliacea do not dominate the zooplankton of coastal upwelling areas since they are such efficient herbivores. Charts of their abundance in the California Current region show that they are dominant only occasionally in upwelling areas although Thaliacea is the principal taxon on a biomass basis for the whole region in the upwelling season (Berner 1967; Isaacs et al. 1969, 1971; Fleminger et al. 1974). They tend to be less abundant close inshore, a situation also observed off northwest Africa in the upwelling season (Blackburn 1979).

The material of the 1969 series of CalCOFI cruises appeared suitable for the proposed distribution study. A large part of the California Current region was covered eight times during 1969 with a similar and rather dense station pattern. The cruises yielded collections and measurements of several properties including zooplankton, chlorophyll *a*, temperature, and surface geostrophic current. Although the CalCOFI program began in 1949, 1969 was the first year of reasonably good coverage for chlorophyll *a* or any other measure of phytoplankton. Thus the charts by Berner (1967) of thaliacean distributions in the period 1949-1958 cannot be related to phytoplankton.

MATERIAL AND METHODS

The materials and data described here refer to all the CalCOFI cruises made in 1969, namely 6901, 6902, 6904, 6905, 6906, 6907, 6908, 6910, and 6912. Figure 1 shows the entire CalCOFI station grid, which, however, was not completely covered on any of the 1969 cruises. The areas actually covered on each cruise are shown with cruise dates in Figures 4 to 20.[2] Within each cruise area all stations shown in Figure 1 were occupied for zooplankton and hydrography, with few exceptions. Chlorophyll *a* was measured at fewer stations. Each station in Figure 1 has a number such as 93.60, where 93 is the identifying number of the line of stations normal to the coast and 60 is the station number within the line. This paper is concerned with lines 60 to 137 (the offing of San Francisco to about 25°N latitude) and stations no farther offshore than number 90, with few exceptions.

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[2]Because the author has made his species distribution charts available in the style and size of the CalCOFI Atlas, we are printing them here full size to facilitate the reader for tearing out and overlaying.

Cruise 6902 extended north of line 60, but none of the others did, and so that part of 6902 was ignored in this study. Cruise 6901 omitted lines south of line 120, and cruise 6904 omitted lines north of line 80. The following cruises or pairs of cruises covered the whole area from line 60 to line 137: 6902, 6905 and 6906 combined, 6907, 6908 and 6909 combined, 6910 and 6912. On 6902 lines 60 to 77 were occupied twice, once by R/V *Miller Freeman* and once by R/V *Alexander Agassiz*. The zooplankton from only the *Miller Freeman* lines, which had more stations, was used in the present work.

Zooplankton Hauls

One oblique non-closing zooplankton haul was made at each station at whatever time it was occupied. Smith (1974) described the methods and charted displacement volumes of total zooplankton in ml/1000 m³ of water strained. The standard haul was from about 210-m depth to the sea surface, but shallower hauls, depending on the depth of bottom, were necessary close inshore. Nets were of uniform mesh size, 0.505 mm. The mean volume of water filtered per standard haul was 672 m³. The actual volumes filtered, haul depths, and other necessary information for all hauls, were obtained from an unpublished list in the computer data files of the Coastal Fisheries Division, Southwest Fisheries Center, National Marine Fisheries Service. The list was kindly provided by Paul Smith.

Sorting and Counting of Thaliacea

Each plankton sample was examined, and large Thaliacea (over 2 cm) were separately counted. The rest of the sample was divided with a Folsom splitter (McEwen et al. 1954) into aliquots of convenient size. The normal aliquot was about 20 to 30 ml. Aliquots were rarely smaller than that but sometimes larger. The sample fraction they represented ranged from 1/4 to 1/128 and was most frequently 1/16. Thaliacea in each aliquot were identified and counted under a low-power microscope. Those numbers were multiplied by the denominator of the aliquot and added to the numbers removed before splitting, to give an estimated number per haul of each species. Thompson (1948) was the principal reference used for identifications.

There were some difficulties in counting, especially when small doliolids were very numerous and entangled in phytoplankton. Some counts were approximate. Special efforts were made to make accurate counts at inshore stations for reasons made clear later. Numbers of different generations (phorozooid and gonozooid in doliolids, solitary and aggregate in salps) were combined because their distributions appeared to be the same. Berner (their distributions appeared to be the same. Berner (1957, 1967) combined generations for the same reason. Aggregates in strings or whorls were counted if separate from

solitaries but not if attached to them. Doliolid oozooids were counted, although not identifiable by species.

The above-mentioned numbers per haul are used in preference to numbers per standard volume of water strained for some purposes, as explained later. The data summarized in Figures 4 to 20 are in numbers per 1000 m³ of water, however. This was done to facilitate comparison with the charts of Berner (1967) for the same region. For the same reasons, I used limiting numbers for contours which are the same as some of Berner's limiting numbers, although my charts have fewer contour intervals. In effect Figures 4 to 20 have less contour detail than similar charts by Berner, but show all important features and can easily be compared with his figures. No contours were drawn around single stations.

Temperature

The principal species of Thaliacea in the California Current region are most abundant near the sea surface, as mentioned later. Berner (1957) compared distributions of Thaliacea and temperatures in the mixed layer. He noted that temperatures measured at 10 m below surface were generally close to mixed-layer temperatures. Berner and Reid (1961) used 10-m temperatures entirely in a similar study, and I have done the same. Wyllie and Lynn (1971) published charts of 10-m temperature for all CalCOFI cruises made in 1969.

Surface Currents

Information on surface currents was obtained from charts of dynamic height anomalies (0 over 500 decibars), prepared for each CalCOFI cruise of 1969. Charts for cruises 6901 and 6902 are given and methods described in Scripps Institution of Oceanography (1976). Those for the other cruises are unpublished and were lent for this study by John Wyllie, who drew them.

Chlorophyll a

Concentration of chlorophyll a as a convenient measurement of total phytoplankton. Owen and Sanchez (1974) listed such concentrations for some stations on each CalCOFI cruise of 1969 and described their methods (fluorometric analysis of acetone extracts). Owen (1974) gave contoured charts of chlorophyll a at the sea surface and in the 0-150-m layer for the four 3-month periods of 1969 (January-March, etc.). His charts show maxima and minima in similar locations for the two depth levels. Remarks made subsequently about chlorophyll distribution refer to the surface data of Owen and Sanchez for the specified cruise. Figures 2 and 3 are based on those data and show areas where surface chlorophyll a was 0.5 mg/m³ or higher on each cruise. Owen and Sanchez also listed data on primary production (C¹⁴ uptake) from some cruises, but the areal coverage was too sparse for the measurements to be of use in this study.

Upwelling Indices

Bakun (1975) calculated mean upwelling indices for each day in 1969 in several areas along the west coast of North America, and some of them are used in this paper. The upwelling index is the component of computed Ekman transport directed offshore, in metric tons of water per sec per 100 m of coastline. Upwelling indices for the inshore end of CalCOFI line 60 were taken from Bakun's table for 39°N latitude, since line 60 was closer to that position than any other position given. Similarly indices for lines 63 to 80 were taken from the table for 36°N; lines 83 to 100 from 33°N; lines 103 to 110 from 30°N; lines 113 to 130 from 27°N; and lines 133 and 137 from 24°N.

RELATIVE ABUNDANCE OF SPECIES

Table 1 is a summary of all data showing numbers per haul by cruise and principal species for northern, central, and southern parts of the area (A, B, and C). The principal species are Salpidæ, except *Dolioletta gegenbauri* and *Doliolum denticulatum* which are Doliolidae.

For the whole area and year the three must abundant forms are *Dolioletta gegenbauri*, *Thalia democratica*, and *Doliolum denticulatum*. They account for 86.4, 6.1, and 2.8%, respectively, of all individuals. Oozooids of Doliolidæ make up an additional 3.2%, which probably represents the above-mentioned species of that family. Salps other than *Thalia democratica*, together with negligible numbers of pyrosome fragments, comprise the remaining 1.5%. Most of this residue (1.3% of the total) is the form known as *Salpa fusiformis*.

In the northern area (San Francisco to Point Conception), the relative abundance of principal species is broadly similar to that for the whole region, except that *Doliolum denticulatum* is scarcer than *Salpa fusiformis*. In the central area (Point Conception to Punta Eugenia), *Dolioletta gegenbauri* is much scarcer than in the north, *Doliolum denticulatum* much more abundant, *Thalia democratica* slightly more abundant, and *Salpa fusiformis* less abundant. Numbers of the first three species are comparable for the year as a whole. South of Punta Eugenia, all species are much scarcer than in the other two areas. *Thalia democratica* and *Doliolum denticulatum* might have been taken in larger numbers if lines of stations had extended as far offshore as in the other areas (Figures 14, 18, and 19). *Thalia democratica, Doliolum denticulatum*, and oozooids in that order comprise 92.8% of the total numbers per haul, and *Dolioletta gegenbauri* is scarcer than *Salpa fusiformis*.

Although *Dolioletta gegenbauri* is predominantly a northern form, it is most abundant in the warmer months wherever it occurs. This suggests that seasonal changes in its abundance might be related to upwelling, although temperature may determine the limits of range. The peak

TABLE 1

Cruises[1], Hauls per Cruise, and
Mean Numbers of Thaliacea per Haul by Species.

Cruise Number	6901	6902	6904	6905 to 6906	6907	6908 to 6909	6910	6912	Total
A. Station Lines 60-77									
Numbers of Hauls	46	58	0	46	47	48	46	47	
Dolioletta gegenbauri	952	242		43,135	11,871	14,021	1,192	284	71,697
Doliolum denticulatum	160	6		<1	<1	36	2	11	215
Oozooids of Doliolidae	182	178		279	332	660	132	28	1,791
Thalia democratica	3	38		1	4	5	0	2,119	2,170
Salpa fusiformis	9	32		8	7	8	130	723	917
Cyclosalpa bakeri	34	7		1	1	0	1	46	90
Iasis zonaria	2	2		8	0	1	0	1	14
Ritteriella picteti	0	<1		1	0	0	0	<1	1
Cycloslapa affinis	1	0		0	0	0	0	1	2
Pegea confoederata	<1	0		<1	0	0	0	1	1
Others[2]	<1	1		<1	0	0	0	0	1
B. Station Lines 80-120									
Number of Hauls	133	126	136	132	136	132	136	133	
Dolioletta gegenbauri	76	68	491	1,069	1,447	236	53	2	3,442
Doliolum denticulatum	184	412	62	25	996	296	60	54	2,089
Oozooids of Doliolidae	79	89	173	112	393	11	19	10	887
Thalia democratica	5	7	4	5	22	8	1,235	1,694	2,980
Salpa fusiformis	10	6	8	18	16	13	47	39	157
Cyclosalpa bakeri	2	1	18	31	0	<1	7	5	64
Iasis zonaria	2	1	<1	<1	<1	<1	<1	1	4
Ritteriella picteti	2	<1	<1	1	<1	<1	<1	0	3
Cyclosalpa affinis	0	0	<1	0	0	0	1	7	8
Pegea confoederata	<1	<1	0	0	0	0	1	2	3
Others[3]	<1	<1	<1	0	<1	1	1	1	3
C. Station Lines 123-137									
Number of Hauls	0	33	31	31	33	33	33	25	
Dolioletta gegenbauri		0	2	0	1	1	0	0	4
Doliolum denticulatum		10	4	0	16	49	14	3	96
Oozooids of Doliolidae		6	37	4	18	15	3	2	85
Thalia democratica		10	18	3	38	24	20	3	116
Salpa fusiformis		1	1	2	1	5	3	1	14
Cyclosalpa bakeri		0	0	<1	0	0	0	0	<1
Iasis zonaria		0	0	0	0	0	0	0	0
Ritteriella picteti		<1	0	0	0	0	0	0	<1
Cyclosalpa affinis		0	0	0	0	0	0	0	0
Pegea confoederata		0	0	0	0	0	0	0	0
Others[4]		0	0	0	0	5	0	0	5

[1]See Figure 1 for location of station lines.
[2]*Cyclosalpa strongylenteron*, *Ihlea punctata*, *Thetys vagina*, plus fragments of *Pyrosoma* colonies.
[3]Same as in [1], plus *Doliolina mülleri*, *Dolioloides rarum*, *Cyclosalpa pinnata*, *Cyclosalpa virgula*, and *Salpa cylindrica*.
[4]*Ihlea punctata*, *Thetys vagina*, and *Salpa cylindrica*.

of the upwelling season in 1969 was March to May in the southern area, April to July in the central area, and June to August in the northern area (Bakun 1975), and this is the usual pattern (Reid et al. 1958). *Doliolum denticulatum* is most abundant in the central area. There seem to be two peaks of abundance, July to September and January to February. *Thalia democratica* is abundant in the central and northern areas but only in October and December. Its peak in the southern area, where it is scarce, in late summer. *Salpa fusiformis*, predominantly northern, is distributed seasonally like *Thalia democratica*. If the three last-mentioned species are related to temperature or upwelling, the relations are probably

more complex than for *Dolioletta gegenbauri*. This matter is discussed later.

The four species mentioned above were also the principal species in the material of Berner (1957, 1967) from the same region. In the rest of this study, only the three most abundant species are considered. The reason for excluding *Salpa fusiformis* is that it may represent a mixture of two species, *S. fusiformis* and *S. aspera*, in the California Current region. Foxton (1961) held this view although others, including Thompson (1948), Berner (1957) and Silver (1975), regarded *S aspera* as an intergrading variety. I could not use the criteria of Foxton to distinguish *fusiformis* and *aspera* under the conditions of my work. The principal criteria are smoothness of the test (spiny or not) and numbers of fibers in muscle-bands. It was common for the test to be found separated from the rest of the animal in the preserved samples, and time was insufficient to count the numerous muscle fibres in all specimens. All specimens were identified as *S. fusiformis*, but in view of Foxton's opinion I hesitate to regard them as one species. Some tests were spiny and some smooth.

Since *Dolioletta gegenbauri*, *Doliolum denticulatum*, and *Thalia democratica* are the only species of those genera considered here, they are henceforth generally referred to by genus only for convenience.

DISTRIBUTION OF PRINCIPAL SPECIES

Dolioletta gegenbauri

Berner (1957) regarded this species as characteristic of subarctic or California Current water. In his material from the region shown in Figure 1, it occurred at stations where mixed-layer temperatures ranged from 9.0° to 27.8°C and averaged 11° to 16°C. Comparing my distribution charts with contemporaneous 10-m isotherms, I concluded that the species generally occurred at <14° in the colder months and <16° in the warmer months. The 15° isotherm seemed to delimit the distribution fairly well on a year-round basis and is shown in Figures 4 to 9.

The non-closing CalCOFI zooplankton hauls give no information on bathymetric distribution of *Dolioletta* or other Thaliacea. Berner (1957) reviewed data from various sources and concluded that *Dolioletta* is most common in the 0-100-m layer, especially at 0-50 m. similar distributions near the sea surface are discussed later for *Doliolum* and *Thalia*. Most hauls were made to about 210 m and strained about 670 m³ of water, as noted earlier. The most inshore one or two hauls on each line were made less deep from necessity, and therefore strained less water. Assuming that each species is concentrated in a layer of more or less uniform depth less than 210 m both offshore and inshore, estimated numbers per 1000 m³ must be high at the inshore stations where shallow

TABLE 2

Rank Correlation Coefficients Between Upwelling Indices and Ratios[1]
of Numbers of *Dolioletta gegenbauri* and *Doliolum denticulatum*
for Two Periods in 1969.

	x	$x-1$	$x-2$	$x-3$	$x-4$	$x-5$	$x-6$
January-June (Cruises 6901-6906)							
Dolioletta gegenbauri	+0.25	+0.29	+0.46**	−0.05	+0.02	+0.06	+0.07
Doliolum denticulatum	+0.21	+0.07	+0.17	+0.22	+0.07	+0.13	+0.19
July-December (Cruises 6907-6912)							
Dolioletta gegenbauri	+0.02	−0.14	−0.11	−0.06	−0.08	−0.17	0.00
Doliolum denticulatum	+0.03	−0.15	−0.15	0.00	−0.26	+0.05	+0.09

[1]Each ratio was the number taken at Station 2 divided by the number at Station 1 where Station 1 was the most inshore station on a CalCOFI line and Station 2 the one next offshore. Each ratio was compared with 7 upwelling indices for the area of the line: x was the index for the day on which the earlier of the two stations was occupied, and $x-1, x-2$, etc., were indices for 1, 2, etc., days previously. Coefficients without * are not significant for the numbers of degrees of freedom used.

hauls were made, relative to such numbers elsewhere. Figures 4 to 20 indicate numbers per 1000 m³ for reasons given earlier, but those within about 10 miles of the coast are too high by an unknown amount.

Figure 4 shows the distribution of *Dolioletta* on cruise 6901 (January 1969). It occurred almost always on the low side of the 15° isotherm, although not in all parts of that area. It was more plentiful inshore than offshore, which was real because the inshore area extended more than 10 miles from the coast. The area of high abundance shown is broadly congruent with the area in which surface chlorophyll was >0.5 mg/m³ (Figure 2, A). The population probably grew faster where food was more plentiful. On cruise 6902 in February-March (Figure 5), the 15° isotherm and the population extended slightly farther south. Figure 2 (B) shows four areas of chlorophyll >0.5 mg/m³ along the coast. *Dolioletta* was relatively abundant in the two northern areas but not in the others, which were probably too warm for it. The small offshore area of abundant *Dolioletta* does not agree so well with chlorophyll concentration, which was low there.

On the April cruise 6904 there were two areas with temperatures <15° at 10 m, one in the main axis of the California Current and one in a coastal upwelling area south of San Diego. The area of occurrence of *Dolioletta* was partially divided in a similar, but not exactly the same, way (Figure 6). In general *Dolioletta* occupied the whole area of <15° water and' extended slightly into warmer water. Chlorophyll >0.5 mg/m³ at the surface occurred almost continuously along the coast (Figure 2, C), and the two high coastal concentrations of *Dolioletta* were in that area. Where *Dolioletta* was missing or scarce near the coast, it was probably because of near-limiting temperatures, with two exceptions: It was absent in a small strip of water near Point Conception and scarce in another strip near San Diego. The temperature was <15° and the chlorophyll >0.5 mg/m³ at both places. Similar situations are seen in other figures and discussed later.

TABLE 3

Data From Which the Significant Coefficient in Table 2[1] Was Calculated.

Cruise	Line	Ratio	Date x	Index
6901	60	2.17	1-24	30
	63	1.47	1-24	49
	80	0.94	1-17	26
	83	5.00	1-17	16
6902	63	3.24	2-8	58
	67	3.45	2-8	58
	70	18.29	2-14	214
	73	2.00	2-15	61
	83	0.84	2-15	86
	90	0.01	2-16	17
	93	1.00	2-16	17
	97	9.00	2-20	167
	100	9.00	2-20	167
	103	2.00	2-23	37
	107	0.03	2-23	37
6904	80	993.00	4-13	93
	83	157.00	4-12	173
	87	3.88	4-10	64
	90	0.43	4-9	34
	93	22.50	4-4	234
	97	26.67	4-2	203
	100	1.63	4-6	42
	103	1.56	4-6	88
	107	3.18	4-9	60
	110	66.40	4-9	60
6905	63	13.00	5-24	132
	67	0.03	5-23	165
	70	0.59	5-22	200
	73	35.20	5-16	130
	77	212.11	5-15	93
	80	4.10	5-13	182
	83	229.82	5-13	264
	87	<0.01	5-10	66
	90	1.61	5-10	66
	93	10.00	5-5	412
6906	97	1.29	6-9	252
	100	129.00	6-12	221
	103	210.00	6-13	88
	107	23.00	6-15	154
	110	<<0.01	6-15	154

[1]Ratio and date x are explained in Table 2; Index is the upwelling index for the second day before date x.

Figure 7 refers to cruises 6905 and 6906 in May and June, north and south of San Diego respectively. The area of 6905 was almost entirely <15°, and *Dolioletta* occurred over nearly all of it. The general level of abundance was higher than before, but the areas of highest abundance did not agree so well with those of high surface chlorophyll, i.e. >0.5 mg/m³ (Figure 2, D). Specifically, *Dolioletta* was absent in an area west of San Diego where chlorophyll was high, perhaps because temperature was ≥15°. It was also less abundant in two coastal strips than it was slightly farther offshore, although chlorophyll was high inshore. These situations, reminiscent of the two noted in April, occurred north of Point Conception and off San Diego. The area of cruise 6906 was >15° except in two coastal upwelling areas.

Dolioletta occurred in the northern upwelling area but not in the southern one, which it probably did not reach even as a seed population. It was present and even moderately abundant in some of the warmer waters as well. The contours run parallel with those of dynamic height. Chlorophyll measurements < 0.5 mg/m³ were in and near the northern upwelling area (Figure 2, D).

The distribution of *Dolioletta* on cruise 6907 (July) is not shown because it was similar to Figure 7. The areas <15° were smaller (Figure 18) but included most of the areas where *Dolioletta* was moderately or very abundant. *Dolioletta* occurred at a low level of abundance in several large areas >15°, as in June. The 15° isotherm followed the limit of the range less well in June and July than in other months. Chlorophyll values for cruise 6907 were mostly <0.5 mg/m³ even along the coast, although higher near the coast than elsewhere (Figure 3, E).

Temperatures on cruise 6908 in August-September (Figure 8) were about the same as on 6907. The southern limit of *Dolioletta* was north of its July position and agreed better with the temperature. A large northern area of relatively high surface chlorophyll (Figure 3, F) included some of the highest concentrations of *Dolioletta*. An elongate area of very abundant *Dolioletta* touched the coast north of Point Conception. At that point the concentration was one of the highest recorded for *Dolioletta*, and the zooplankton was almost entirely that species. On cruise 6909 (September-October, south of San Diego) almost all waters were >15°, and *Dolioletta* was scarcely present (Figure 8). High temperature probably excluded it. Surface chlorophyll was high along the coast north of Punta Eugenia (Figure 3, F).

On cruise 6910 (October-November) the total area of *Dolioletta* and water <15° was about the same as in Figure 8, but *Dolioletta* was generally scarcer (Figure 9). Figure 3(G) shows the distribution of chlorophyll >0.5 mg/m³, which agreed fairly well with that of *Dolioletta* in inshore waters. The distribution on cruise 6912 (November-December) is not shown. It was much more restricted than on any other cruise, in an area off San Francisco and a small one of low abundance on the coast east of Point Conception. The first area was in water <15° and the second was not (see temperature in Figure 20). Chlorophyll concentrations >0.5 mg/m³ were virtually confined to the San Francisco area (Figure 3, H).

Figures 4 to 9 are broadly similar to some of the charts of Berner (1967) for *Dolioletta* at the same periods in other years. For example, Figures 5, 7, and 8 are comparable with those for the same periods in 1950, 1950, and 1949 respectively. On the other hand, Figures 8 and 9 do not agree well with those for the same periods in 1952, when *Dolioletta* was fairly abundant south of Punta Eugenia.

Doliolum denticulatum

Berner (1957) and Berner and Reid (1961) considered this species characteristic of Central Pacific water, which contributes to the California Current by horizontal mixing from the west (Reid et al. 1958). Thus *Doliolum* enters the current system from the west, not from the north as *Dolioletta* does. In Berner's material from the region of Figure 1, it occurred at stations where mixed-layer temperatures ranged from 10.6° to 23.5°C and averaged 15° to 21°C. Berner and Reid considered its areal distribution to be limited by some 10-m temperature slightly below 14° or 15°. They used the 14° isotherm at 10 m as an indicator of the limit of distribution. In their charts and mine, the winter occurrence of *Doliolum* can be quite extensive on the cool side of the 14° and even the 13° isotherm. The 13° isotherm seems to delimit the distribution better than any other throughout the year and is shown in Figures 10 to 14. Data on vertical distribution from various sources indicate that *Doliolum* is most common at 0-100 m, especially 0-50 m (Berner 1957; Berner and Reid 1961). Thus concentrations shown in Figures 10 to 14 at stations very close inshore are too high relative to those at other stations for reasons given under *Dolioletta*.

Figure 10 shows the distribution of *Doliolum* in January. It occurred in several inshore and offshore areas at >13° and extended north along the coast in slightly cooler water. The area of higher abundance is similar to that of surface chlorophyll >0.5 mg/m³ (Figure 2, A) but extends farther south along the coast. The general picture is like that shown by Berner and Reid (1961) for January 1958. They regarded the coastal occurrence north of Point Conception as unusual, since it was not seen in earlier winters for which they had data (Berner 1967). They attributed it to transport in the countercurrent, which runs poleward close to the coast in winter. This countercurrent was present in January 1969 but only north of San Diego (Scripps Institution of Oceanography 1976). Together with the temperature and chlorophyll data, it explains the observed distribution of *Doliolum* in inshore waters, including the break south of San Diego.

In February-March (Figure 11) *Doliolum* occurred less extensively to the north of Point Conception than in January. although surface concentrations of chlorophyll >0.5 mg/m³ were still present (Figure 2, B). The countercurrent was weaker and probably brought in a smaller seed population. The rest of the distribution is consistent with the idea of a population spreading in from offshore, being limited to waters >13°, and increasing in numbers in coastal locations of relatively high chlorophyll. The areas of relatively abundant *Doliolum* broadly agree with the areas of high chlorophyll, except for one of the latter south of Punta Eugenia. Figure 11 resembles the

chart for March 1958 but is quite unlike that for March 1949 when no *Doliolum* occurred inshore (Berner and Reid 1961). Berner and Reid pointed out that temperatures were higher in 1958 than in the years 1949 to 1956.

The distribution of *Doliolum* for April is not shown here. The species occurred in patches over most of the area from Point Conception to Punta Eugenia, both offshore and inshore, where almost all temperatures were >13°. Highest concentrations were close to the coast in areas of high chlorophyll, which are shown in Figure 2, C. The chart for April 1958 by Berner and Reid is comparable but shows a more continuous distribution over the same area. Charts for April of 1949 and 1954 show no inshore occurrence (Berner 1967).

Figure 12 is for May and June. Most of the area was >13°, but *Doliolum* was scarce, being most abundant in an upwelling area north and south of San Diego where surface chlorophyll was >0.5 mg/m³ (Figure 2, D). Most other high-chlorophyll areas were in inshore waters north of Point Conception, which were probably too cool for *Doliolum*. As noted for *Dolioletta* in Figures 6 and 7, abundance sometimes fell at the most inshore stations. For *Doliolum* this could be caused by low temperature from the upwelling. That would not apply to *Dolioletta*, however, and another explanation is suggested later. Figure 12 shows a distribution much less extensive in inshore waters than in May 1958, but more than in June 1949 (Berner and Reid 1961). The connections between offshore and inshore occurrences seem to have been reduced from a few months earlier (compare with Figures 10 and 11).

The July chart (Figure 13) reveals a more extensive and continuous distribution, although by no means covering the whole area of water >13°. That isotherm delimits the range of *Doliolum* better in cold months than in warm. Abundance was highest along the coast and so in general were the chlorophyll concentrations, but they were lower than usually found with the higher concentrations of doliolids (Figure 3, E). The only other published July chart is for 1949 (Berner 1967), which shows no inshore occurrences.

The chart for cruises 6908 and 6909 (August-October) is similar to Figure 13 and the following Figure 14 and so is not given. It also resembles the situation for September 1952 but not for September 1949 (Berner and Reid 1961). The distribution of *Doliolum* on cruise 6908 (north of San Diego) agreed well with that of chlorophyll, both being relatively abundant in certain inshore waters. The agreement on 6909 (south of San Diego) was poor, however. Figure 3(F) shows the areas of highest chlorophyll.

The October-November distribution (Figure 14) is much the same as the preceding. It resembles those of October-November 1951, 1952, and 1957 but not 1949

(Berner and Reid 1961; Berner 1967). It agrees only partially with chlorophyll distributions (Figure 3, G). The chart for November-December (not given) shows *Doliolum* ranging farther north along the coast from Point Conception, recalling the situation in Figure 10. The countercurrent was not evident on cruise 6912, although it was on the preceding one. *Doliolum* was scarcer on 6912 than on cruises 6910 or 6901. Agreement between areas of high chlorophyll and abundant *Doliolum* was poor. The richest area of chlorophyll was in the offing of San Francisco (Figure 3, H), and *Doliolum* did not reach it.

Concentrations of *Doliolum* were generally lower than those of *Dolioletta* in 1969. Maximum numbers per haul were respectively 48,000 and 264,000. No plankton sample consisted almost entirely of *Doliolum*, but a few samples were almost totally *Dolioletta* or *Thalia*.

Thalia democratica

According to Berner (1957) this is a species of Central Pacific water. It enters the California Current system by horizontal mixing from the west, like *Doliolum*. In Berner's material it occurred at stations where mixed-layer temperatures ranged from 10.0° to 24.9°C and averaged 14° to 21°C. It appeared from inspection of all 1969 data that the 15° 10-m isotherm delimited the distribution of *Thalia* better than any other, and it is shown in Figures 15 to 20. *Thalia* is most common on the warm side of that isotherm and *Dolioletta* on the cool side. The distribution of *Thalia* is in some ways like that of *Doliolum*, but it appears to be slightly less tolerant of cool water and occurs less often at the coast. According to Berner (1957) and the authors he cited, *Thalia* is most common at 0-75 m, especially 0-25 m. Thus, previous remarks about inshore concentrations apply also to this species.

Figures 15 and 16 show distributions of *Thalia* in January and February-March. In these and later figures the contour intervals are not the same as previously used. The species occurred mainly offshore and, unlike *Dolioletta* and *Doliolum*, it hardly ever reached the coast. Thus, its occurrences do not agree at all with those of relatively high chlorophyll concentrations (Figure 2, A and B). *Thalia* was found in areas where surface chlorophyll ranged from 0.1 to 0.3 mg/m³ (data of Owen and Sanchez 1974). Charts by Berner (1967) for February and March 1949, 1951, 1952, and 1954 are comparable with Figure 16, but in 1950 *Thalia* was much more abundant and widespread and reached several parts of the coast. Distributions for April 1969 (not given) and May-June (Figure 17) were broadly like the preceding but with diminishing occurrence of *Thalia* on the cool side of the 15° isotherm. Relations to chlorophyll (Figure 2, C and D) were about the same as before. Abundance of *Thalia* for the whole area remained at the low levels of

previous months. Berner's (1967) charts of *Thalia* in those months show similar conditions in 1949 but a more widespread distribution and higher abundance in 1950, 1951, 1952, 1954, and 1958.

The July chart (Figure 18) and that for August-October (not given) are alike. They show a slight increase in general abundance of *Thalia*, which occurred over larger areas and sometimes closer to the coast. The 15° isotherm agreed much better with the limits of range of *Thalia* than before and did so for the rest of the year. Surface chlorophyll concentrations in *Thalia* areas were quite low, generally <0.1 mg/m³ (compare Figure 3, E and F). Distributions of *Thalia* in the same months in 1949, 1951, and 1952 showed some occurrence in coastal waters south of San Diego, but this was not so in 1950 (Berner 1967).

Figures 19 and 20, for October-November and November-December, reveal a wider distribution and much higher general abundance than in other months. *Thalia* reached the coast at several places, although the highest concentrations (maximum 56,000/haul) were offshore in chlorophyll-poor areas. At a few of those stations, the zooplankton was almost entirely *Thalia*. There were a few areas of chlorophyll >0.5 mg/m³ in water >15° (Figure 3, G and H), but *Thalia* did not occur in them. Berner (1967) gave charts for October-November of 1949, 1951, and 1952. They are similar to mine except that some of the highest concentrations extended to the coast south of San Diego. Temperature charts for those periods show no signs of upwelling at the places where *Thalia* was abundant inshore (Anonymous 1963), so chlorophyll was probably low.

ABUNDANCE RELATED TO UPWELLING INDEX

It was noted earlier that *Dolioletta* and *Doliolum* sometimes declined in abundance at the innermost one or two stations of a line. Figures 6, 7, and 12 show this. More instances might be evident but for the fact that numbers per 1000 m³ tend to be relatively high at inshore stations, as explained previously. Since chlorophyll concentrations were generally highest close inshore (Figures 2 and 3), it seemed that some other property or process at times depressed the inshore abundance of doliolids.

In upwelling situations along the coast, 10-m temperatures were often about 13°C, and occasionally as low as 11°C (Wyllie and Lynn 1971). From previous information, such temperatures would not have been unsuitable for *Dolioletta*, but they would have been slightly adverse for *Doliolum*. Another possibility is that offshore Ekman transport of near-surface water prevented the animals from becoming more abundant close inshore. Since both possibilities are associated with upwelling, it was decided to investigate the relations of inshore abundance to contemporaneous upwelling indices in the same area. Data on abundance of *Dolioletta* and *Doliolum* were used. *Thalia* seldom occurred inshore.

The number of the species taken at the most inshore station was divided into the number at the station next offshore. The distance between the stations ranged from 4 to 16 nautical miles and averaged 6.9 miles. If one of the two stations had a zero number, 1 was added to each of the two numbers so that a ratio could be obtained. Then, for each line upwelling indices were found from Bakun (1975) for each of the following days: x, the day on which the earlier of the two stations was occupied; $x - 1$, the previous day; $x - 2$, the day before that; and so on to $x - 6$. The two stations were generally occupied on the same day and were never more than one day apart. Negative or zero values of the upwelling index were not used. The data are copious, and it is only necessary to give them in one case, which serves as an example (Table 3). A Spearman rank correlation coefficient was calculated for each set of paired ratios and indices.

Table 2 lists the 28 correlation coefficients for the two species for January-June and July-December. Only one is statistically significant, but the probability of as high a value by chance is <1%, so the significance is not questionable. Furthermore, the date in that case of the upwelling ($x - 2$) in relation to the date of the observations is reasonable. Typical values for offshore transport near the surface in coastal upwellings are about 10 to 25 cm/second when winds are strong (Huyer 1976). Thus, it would take one or two days for a parcel of water and plankton to be moved from one station to the other. The coefficients for the earlier period are nearly all positive, and those for the later period nearly all negative. Numbers of pairs of observations for January-June ranged from 36 to 43 for *Dolioletta* and from 27 to 33 for *Doliolum*. For July-December the corresponding ranges were 35 to 39 and 41 to 43. It may be concluded that the offshore:inshore ratio of abundance of *Dolioletta* in January-June is positively correlated with the amount of upwelling about two days before the observations. A similar correlation may exist for *Doliolum* at the same period but cannot be demonstrated. No such correlations are found for either species in July-December.

DISCUSSION

The distribution of *Dolioletta gegenbauri* seems to be governed by temperature, food (phytoplankton), and water movements in a rather simple way. The southern limit of its range is obviously temperature-dependent. Since it enters the region of interest from the north with the California Current, rather than from offshore, it is always present fairly close to shore in waters of suitable temperature. Thus, it can become abundant fairly quickly in areas where phytoplankton is most plentiful, which are mostly coastal upwelling areas. Most of the observa-

tions are consistent with such growth of population (Figures 4 to 9) in food-rich areas (Figures 2 and 3). A few of the observations are inconsistent, and they cannot all be explained. Some can, as indicated in the previous section. In the first half of the year there is a statistically significant tendency for the offshore:inshore ratio of *Dolioletta* numbers to vary positively with the upwelling index. That is to say, abundance close inshore is lower than expected as a result of the upwelling. The upwelling does not affect the distribution of *Dolioletta* through the low temperature, which that species can tolerate. It probably affects the distribution by transporting some individuals offshore, or retarding the spreading of more offshore individuals toward the shore. After June, however, it is apparently easier for *Dolioletta* to reach very high levels of abundance in food-rich situations close inshore. Upwelling indices begin to decline about that time on the southern and central parts of the coast (Bakun 1975), and the offshore Ekman transport is probably less effective than formerly in depressing numbers of *Dolioletta* close inshore.

The range of *Doliolum denticulatum* is also limited by temperature, as Berner and Reid (1961) pointed out. It occurs with higher temperatures than does *Dolioletta*. The relation to temperature is not as obvious in Figures 10 to 14 as in charts for *Dolioletta*, because there are generally large areas with suitable temperature where *Doliolum* does not occur. *Doliolum* enters the area from the west and reaches the coast as a result of horizontal mixing of waters. When it reaches the coast the population may increase in response to the high abundance of phytoplankton in inshore waters, as with *Dolioletta*. There are more exceptions, however. A few of them very close inshore probably signify effects of low temperatures caused by upwelling. Some may represent effects of offshore Ekman transport, operating as shown above for *Dolioletta*. Some in winter can be explained as a result of transportation along the coast by the countercurrent, as noted also by Berner and Reid (1961). There still remain several unexplained instances of apparent failure of *Doliolum* to become abundant along all parts of the coast where food and temperature conditions are suitable. The reason may be that the species often fails to reach the coast at all, which is much better shown in some charts of Berner and Reid for certain years than in mine. I interpret the distribution in Figure 12, showing discontinuous occurrence from offshore to inshore in May and June, as meaning that the velocity of the California Current posed a barrier to the eastward spreading of *Doliolum*. The current then had a higher velocity and was less meandering than in other months of 1969, a situation seen also in monthly average charts (Wyllie 1966).

Berner and Reid (1961) observed that *Doliolum* extended from offshore to inshore much more frequently in

1957 and 1958 than in the period 1949 to 1955 and that the 1957-58 winter was the first one known to them in which some *Doliolum* remained inshore. They considered these changes to be related to the anomalously high temperatures of late 1957 and 1958. The distributions in 1969 were more like those of 1957 and 1958 than the other years. Temperatures in the California Current region in 1969 were not high as in 1957 and 1958, however, but average (Anonymous 1963; Wyllie and Lynn 1971).

The distribution of *Thalia democratica* is hard to explain. It enters the area from the west like *Doliolum*, and its range from north to south is broadly temperature-dependent in much the same way as that of *Doliolum*. Unlike *Dolioletta* and *Doliolum*, it does not become very abundant or reach the coast until October-December, which is after the upwelling season (Figure 15 to 20). Even then the highest concentrations of *Thalia* remain offshore in areas where chlorophyll values are quite low. According to the charts of Berner (1967), the situation in other years of observation was probably not very different, although no chlorophyll data are available.

Silver (1971, 1975) made observations on stomach contents of *Thalia* and concluded that *Thalia* swarms were associated with a certain assemblage of phytoplankton species in the water. If that assemblage were characteristic of offshore rather than inshore waters in the California Current region, it could be argued that it governs the distribution of *Thalia*. The matter is questionable, however. Silver identified only four species by name, *Nitzschia sicula*, *N. bicapitata*, *Pseudoeunotia doliolus*, and *Thalassionema nitzschoides*. According to Elizabeth Venrick (personal communication), *N. sicula* is frequent but not abundant in offshore waters, and little is known about its abundance inshore; *N. bicapitata* is ubiquitous in distribution; *P. doliolus* can be abundant offshore, and little is known about its abundance inshore; and *T. nitzschoides* is more or less ubiquitous but slightly more abundant inshore.

Harbison and Gilmer (1976) found that salps have the same rates of filtration at different particle concentrations. They also noted that the mucous feeding net became clogged with particles in some of their experiments, which lasted from 2 to 9 hours. They therefore believed that salps would clog in areas of very rich phytoplankton and could not become highly abundant there. The distribution of *Thalia* as shown here might be reconciled with that idea. On the other hand, Heron (personal communication) has found that salps regularly cease production of the mucous net, which might eliminate or relieve clogging. Doliolids can be very abundant in phytoplankton-rich areas as shown in this paper. Clogging has not been reported in them.

The specific question posed at the beginning of the paper was why Thaliacea do not generally dominate the

zooplankton in coastal upwelling situations in the California Current region. For *Dolioletta gegenbauri*, the answer is that offshore Ekman transport prevents the species from becoming dominant in the early part of the upwelling season, although it sometimes does become dominant later. The answer for *Doliolum denticulatum* is probably that the velocity of the California Current makes it hard for the species to reach the coast from offshore in the upwelling season; and when it does arrive it is sometimes excluded from the inshore waters by very low temperature, and perhaps also by the offshore transport. No explanation can be given with confidence for *Thalia democratica*, but a possible one is that the most suitable diet consists of species of phytoplankton that generally occur offshore.

ACKNOWLEDGMENTS

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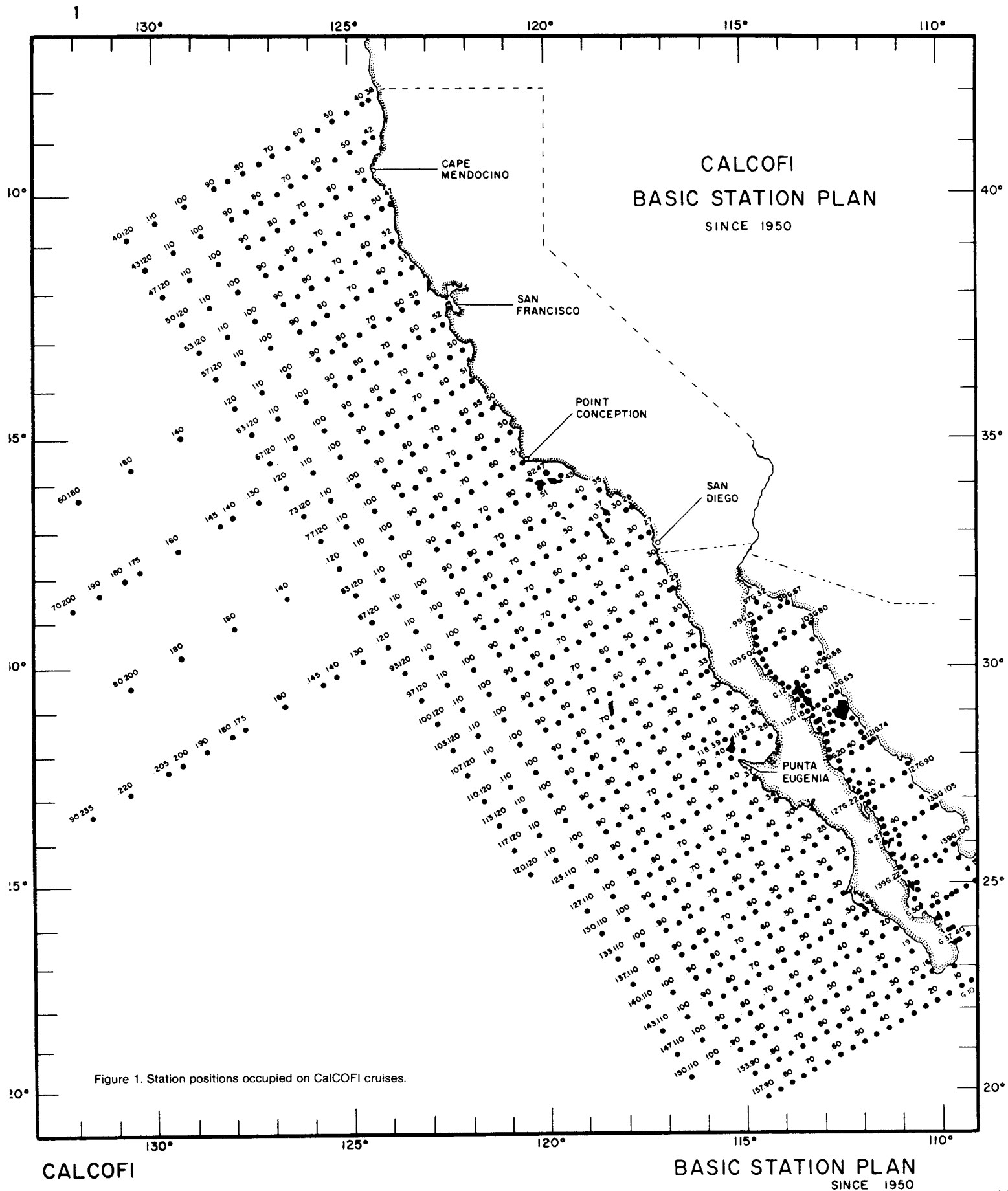
CALCOFI
BASIC STATION PLAN
SINCE 1950

Figure 1. Station positions occupied on CalCOFI cruises.
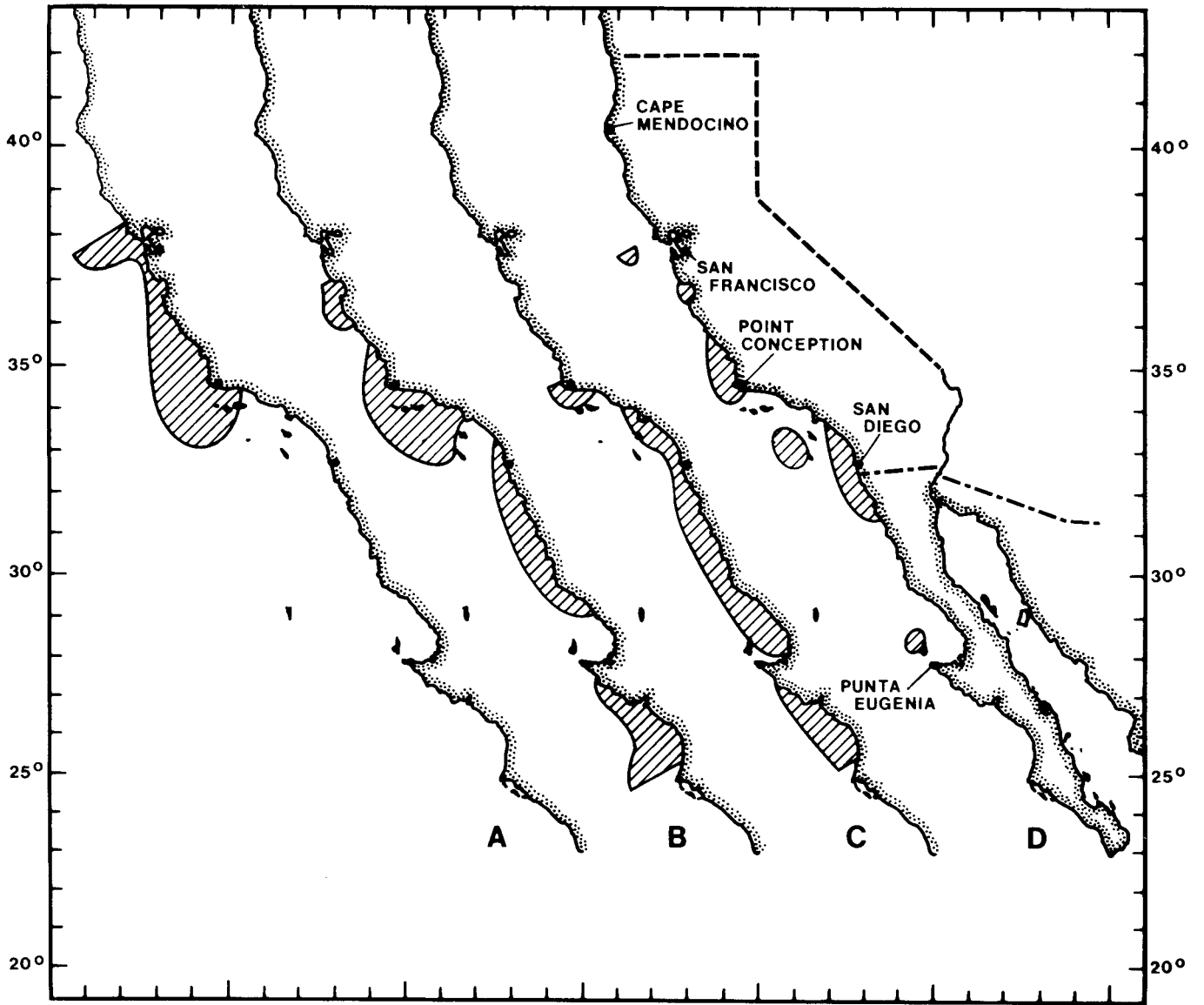
Figure 2. Areas of surface chlorophyll a ≥0.5 mg/m³ shown by hatching on the following CalCOFI cruises: 6901 (A), 6902 (B), 6904 (C) and 6905-6906 (D).
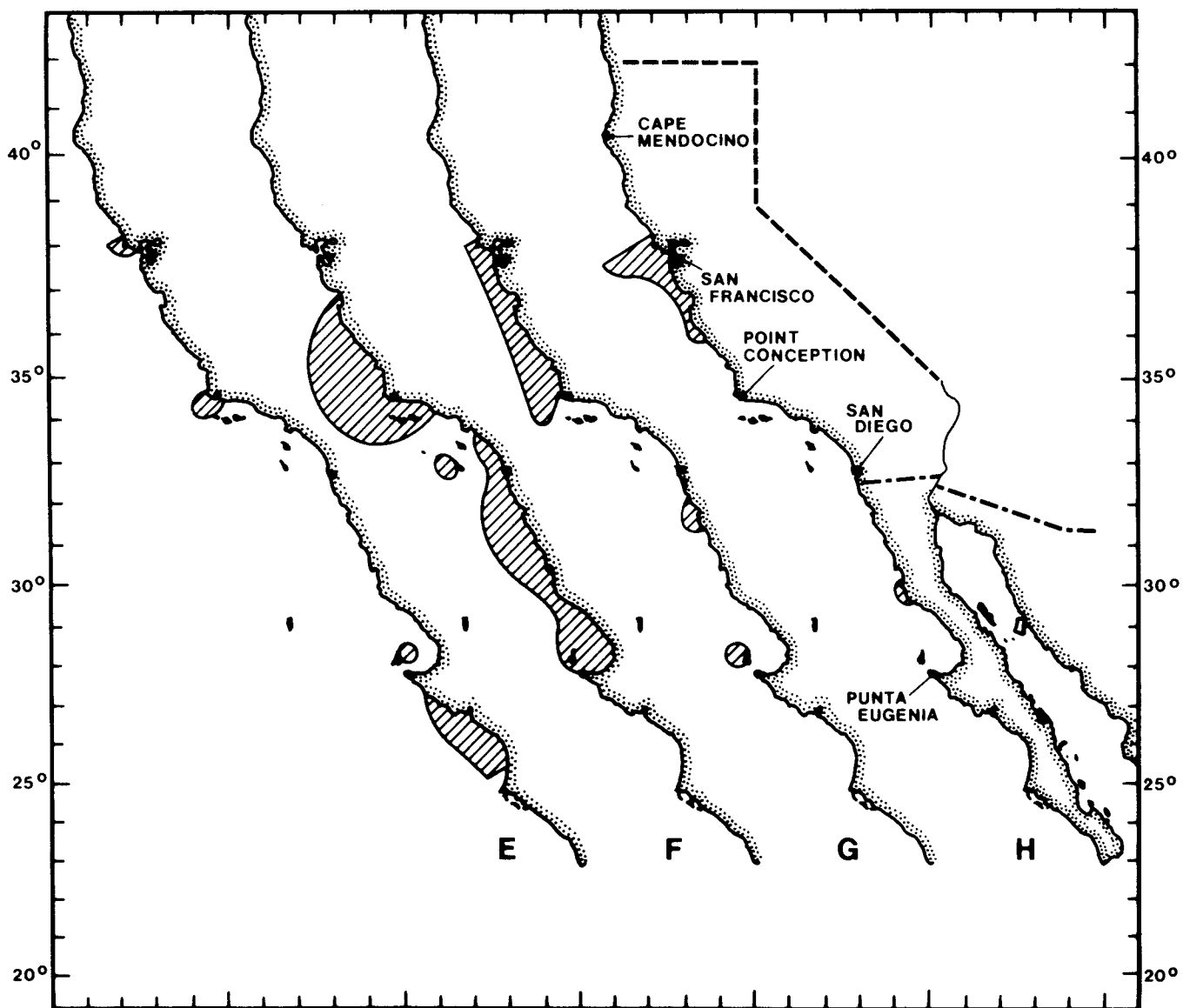
Figure 3. Areas of surface chlorophyll a ≥0.5 mg/m³ shown by hatching on the following CalCOFI cruises: 6907 (E), 6908-6909 (F), 6910 (G) and 6912 (H).

Figure 4. Distribution of *Dolioletta gegenbauri* on CalCOFI cruise 6901.
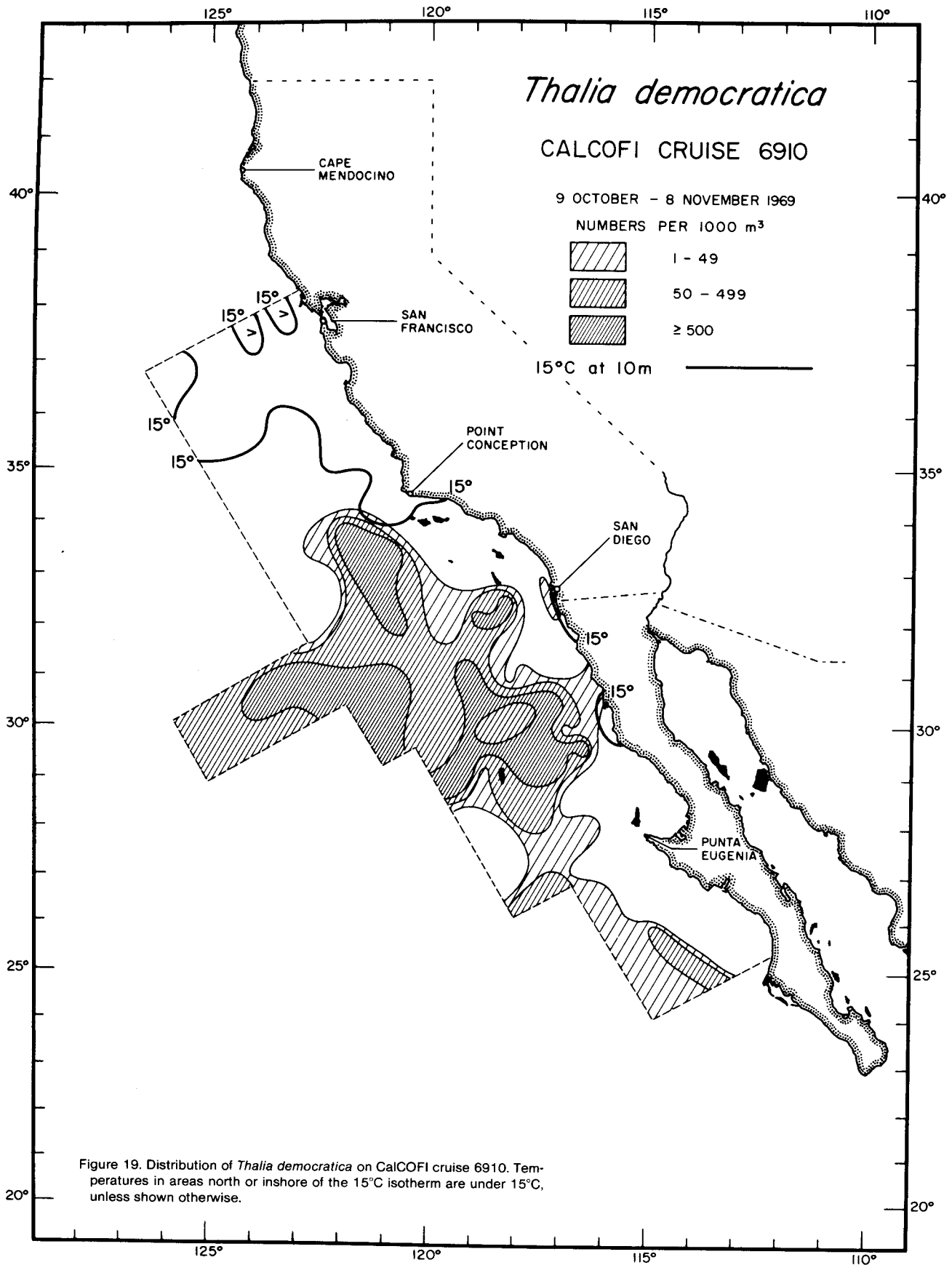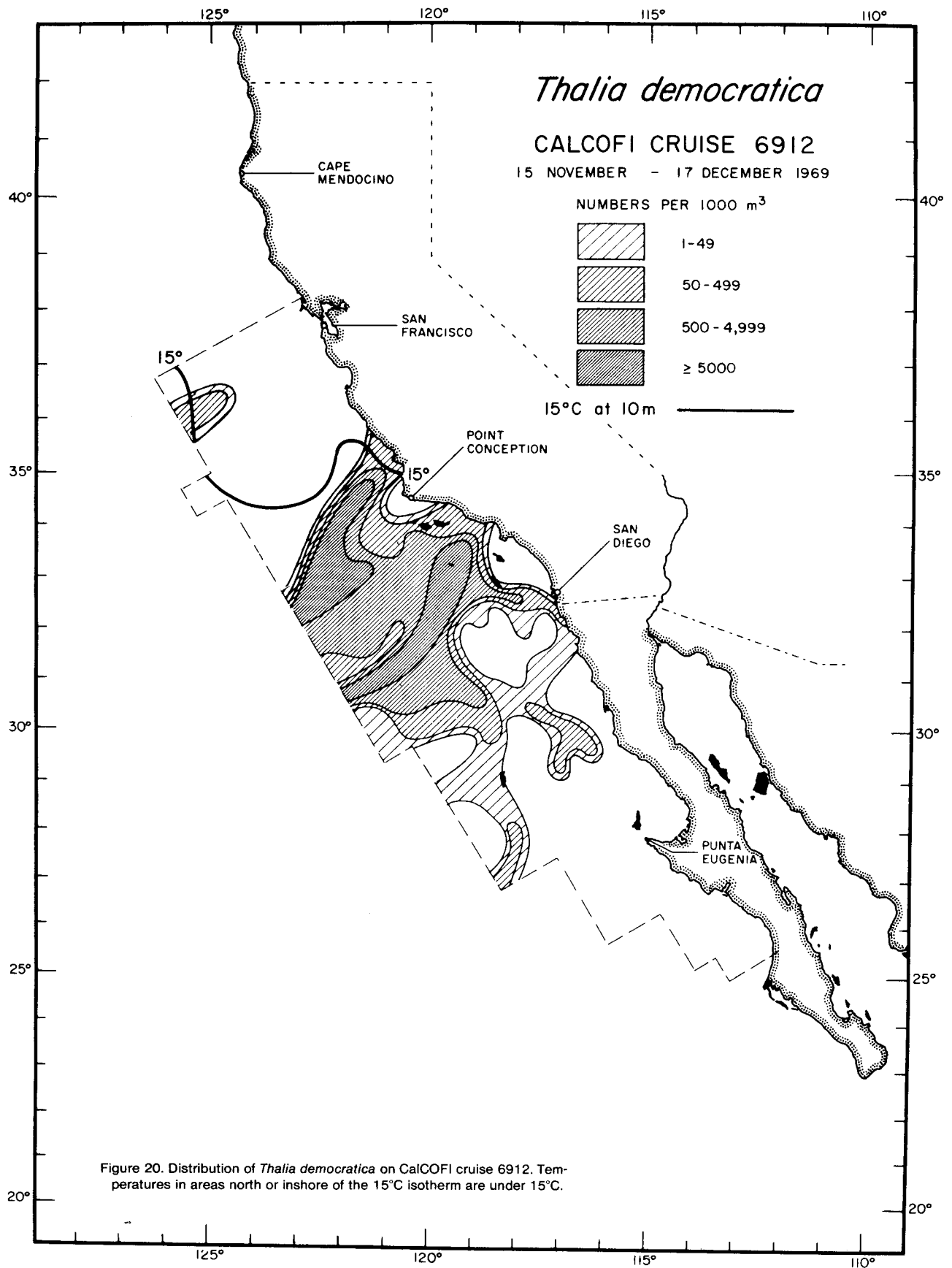Temperatures in areas north of or enclosed by the 15° C isotherm are under
15° C.

Figure 5. Distribution of *Dolioletta gegenbauri* on CalCOFI cruise 6902. Temperatures in areas north or inshore of the 15° C isotherm are under 15° C.

Figure 6. Distribution of *Dolioletta gegenbauri* on CalCOFI cruise 6904.
Temperatures in areas north or inshore of or enclosed by the 15° C isotherm
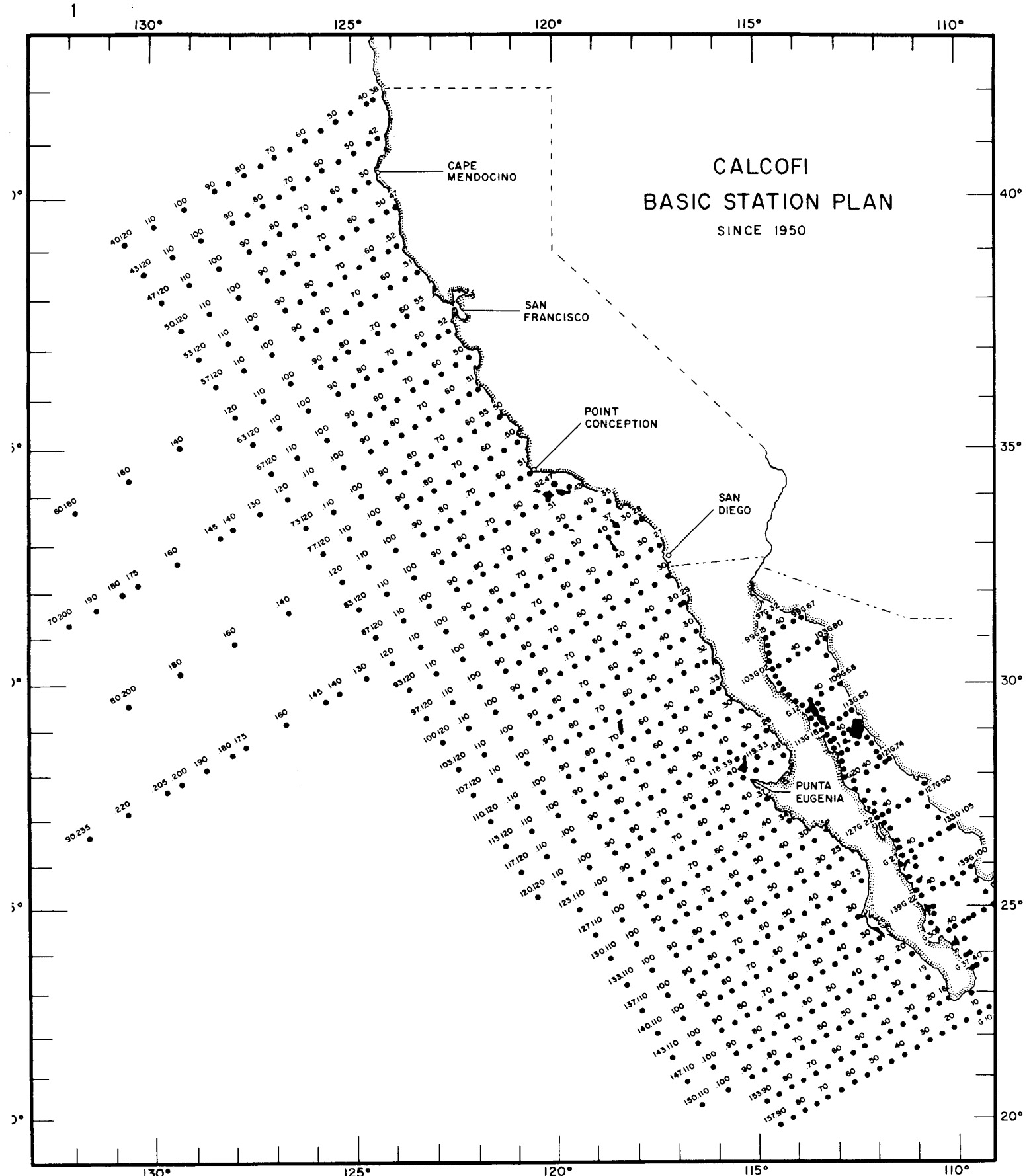are under 15° C unless shown otherwise.

Figure 7. Distribution of *Dolioletta gegenbauri* on CalCOFI cruise 6905 and 6906. Temperatures in the 6905 area are under 15°C unless shown otherwise. Temperatures in the 6906 area are over 15°C except inshore of the 15°C isotherm.

Dolioletta gegenbauri

CALCOFI CRUISE 6908
8 AUGUST – 8 SEPTEMBER 1969

CALCOFI CRUISE 6909
11 SEPTEMBER – 6 OCTOBER 1969

NUMBERS PER 1000 m³

	1 – 499
	500 – 49,999
	≥ 50,000

15°C at 10m ────────

Figure 8. Distribution of *Dolioletta gegenbauri* on CalCOFI cruises 6908 and 6909. Temperatures in areas north or inshore of or enclosed by the 15 C isotherm are under 15 C.

Dolioletta gegenbauri

CALCOFI CRUISE 6910

9 OCTOBER – 8 NOVEMBER 1969

NUMBERS PER 1000 m³

1 – 499

500 – 49,999

15°C at 10m

Figure 9. Distribution of *Dolioletta gegenbauri* on CalCOFI cruise 6910.
Temperatures in areas north or inshore of the 15 C isotherm are under
15 C.

Doliolum denticulatum

CALCOFI CRUISE 6901

7 – 29 JANUARY 1969

NUMBERS PER 1000 m³

1 – 499

500 – 49,999

13°C at 10m

Figure 10. Distribution of *Doliolum denticulatum* on CalCOFI cruise 6901.
Temperatures in areas north of the 13° C isotherm are under 13° C.

CAPE MENDOCINO

SAN FRANCISCO

POINT CONCEPTION

SAN DIEGO

PUNTA EUGENIA

13°

Figure 11. Distribution of *Doliolum denticulatum* on CalCOFI cruise 6902.
Temperatures in areas north of or enclosed by the 13° C isotherm are under
13° C.

Figure 12. Distribution of *Doliolum denticulatum* on CalCOFI cruises 6905 and 6906. Temperatures in areas inshore of the 13° C isotherm are under 13° C.

Doliolum denticulatum

CALCOFI CRUISE 6907

9 – 29 JULY 1969

NUMBERS PER 1000 m³

1 – 499

500 – 49,999

13°C at 10m

Figure 13. Distribution of *Doliolum denticulatum* on CalCOFI cruise 6907. Temperatures in areas north or inshore of the 13° C isotherm are under 13° C.

Figure 14. Distribution of *Doliolum denticulatum* on CalCOFI cruise 6910.
Temperatures in areas inshore of the of the 13° C isotherm are under
13° C.

Figure 15. Distribution of *Thalia democratica* on CalCOFI cruise 6901. Temperatures in areas north of or enclosed by the 15° C isotherm are under 15 C.

Figure 16. Distribution of *Thalia democratica* on CalCOFI cruise 6902. Temperatures in areas north or inshore of the 15° C isotherm are under 15° C.

Thalia democratica

CALCOFI CRUISE 6905
5-26 MAY 1969

CALCOFI CRUISE 6906
9-28 JUNE 1969

NUMBERS PER 1000 m³

1 - 49

50 - 499

15°C at 10m

Figure 17. Distribution of *Thalia democratica* on CalCOFI cruises 6905 and 6906. Temperatures in the 6905 area are under 15°C unless shown otherwise. Temperatures in the 6906 area are over 15°C except inshore of the 15°C isotherm.

Figure 18. Distribution of *Thalia democratica* on CalCOFI cruise 6907. Temperatures in areas north or inshore of or enclosed by the 15° C isotherm are under 15° C.

Figure 19. Distribution of *Thalia democratica* on CalCOFI cruise 6910. Temperatures in areas north or inshore of the 15°C isotherm are under 15°C, unless shown otherwise.

Figure 20. Distribution of *Thalia democratica* on CalCOFI cruise 6912. Temperatures in areas north or inshore of the 15°C isotherm are under 15°C.

CALCOFI
BASIC STATION PLAN
SINCE 1950

CAPE MENDOCINO

SAN FRANCISCO

POINT CONCEPTION

SAN DIEGO

PUNTA EUGENIA

CONTENTS